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Study of Snake Populations in Central California

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INTRODUCTION

Investigations of rodent populations on range lands of the Sierra Nevada foothills in central California led to a study of predators, including snakes, to determine the role of predation in rodent ecology. The feeding habits, abundance, seasonal activity, and movements of several snake species were investigated in an area where vegetation and rodent populations were being studied concurrently. Here the rattlesnake (*Crotalus viridis*) was found in greater numbers than all other species combined. The gopher snake (*Pituophis catenifer*), king snake (*Lampropeltis getulus*), and garter snakes (*Thamnophis elegans* and *T. ordinatus*) were also recorded in sufficient numbers to yield significant data. The racer (*Coluber lateralis*), night snake (*Hypsiglena ochrorhyncha*), long-nosed snake (*Rhinocheilus lecontei*) and ring-necked snake (*Diadophis amabilis*) were found only in small numbers and but little was learned concerning them.

Beginning in May 1938, all snakes that could be secured on the 4600 acre experimental area were recorded as to size, sex, weight, and exact location.

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Nearly all of those that were caught alive were individually marked for future recognition (using essentially the same technique employed by Blanchard and Finster, 1933) and released. Feeding records were obtained whenever possible, through direct observation in the field, dissection of dead snakes, and palping of the live ones that were marked and released. The study was carried on through 1938, 1939, 1940, and March and April 1941. Thereafter, during the war years it was discontinued but in 1946 and 1947, 35 marked snakes of three different species were recaptured after intervals of 5 to 9 years, providing additional records of unusual significance.

This work was done in collaboration with the U. S. Forest Service, California Forest and Range Experiment Station, on the San Joaquin Experimental Range near O'Neals, Madera County. Everett E. Horn of the U. S. Fish and Wildlife Service was in charge of this project and did much to further its progress. Especial gratitude is due to Freeman Swenson for his donation of many live snakes and valuable field observations. Ben Glading helped with the work in its early stages, and participated in the preparation of a preliminary report on the rattlesnakes. Howard Twining analyzed scatological material. Arnold Snyder made available a record and photograph of a king snake feeding. Roy Saarni obtained several outstanding records. Dr. Laurence M. Klauber kindly consented to read the manuscript, and, drawing on his wide knowledge of snakes in general and rattlesnakes in particular, made criticisms and suggestions which aided materially in interpreting data. Wade Fox, C. B. Perkins and Charles E. Shaw likewise read the manuscript and offered helpful suggestions and criticisms. Numerous other persons furthered the field work by contributing snakes either dead or alive, and by helping in many other ways.

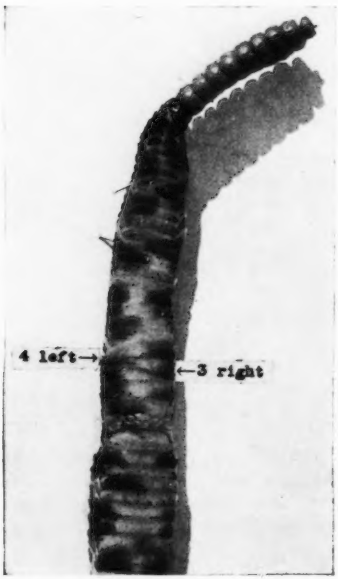

Fig. 1.—Ventral view of tail of the marked rattlesnake (4 left, 3 right); illustrates method of marking and appearance of scars after a 106-month interval.

Certain data and conclusions from this study already have been set forth in several preliminary papers (Horn and Fitch, 1942; Fitch and Twining, 1946; Fitch and Glading, 1947). In a few instances more extensive data have changed earlier conclusions — particularly with reference to the population density and movements of rattlesnakes. Thus the present paper is to be regarded as superseding the earlier ones in any instances where figures or statements differ.

ENVIRONMENT

The San Joaquin Experimental Range, where this study was made, lies in the blue oak (*Quercus douglasii*)-Digger pine (*Pinus sabiniana*) woodland belt characteristic of the foothill region encircling the Sacramento-San Joaquin Valley. The interior live-oak (*Quercus wislizenii*) is common, as also are various chaparral species. The terrain is rolling, with some open grassland, shallow rocky soil, and frequent outcrops of granite rock, often in extensive piles. The flora is predominantly one of annual forbs and grasses with a winter and spring growing season, and a long, hot, dry season during summer and fall.

Numerous rodent and lizard species provide the main foods of the snake populations. The largest animal preyed upon is the cottontail rabbit (*Sylvilagus audubonii*), which was abundant locally with summer populations of between .6 and .7 per acre in 1940, and considerably more in 1939 and 1941. The largest rodent is the California ground squirrel (*Citellus beecheyi*), which is also one of the more abundant species, and a favorite prey of many kinds of predators. Its breeding population over the Range as a whole during the time of the study was approximately 1.5 per acre, with increase to at least three times that number in spring as the result of a late winter annual breeding season. The woodrat (*Neotoma fuscipes*) occurs in populations of several to an acre, at times, in the more brushy situations, but no figures are available as to its numbers on large areas. The pocket gopher (*Thomomys bottae*) is probably the most abundant of the rodents, if not of all vertebrates. Attempts to census it by counting fresh workings or by trapping out small areas were not altogether satisfactory but indicated populations of from eight or nine to more than twenty per acre. Numbers are highest in late spring, when there is a high percentage of young. There may be two or more litters annually. The kangaroo rat (*Dipodomys heermanni*) occurred in changing population densities of less than four to more than seven per acre according to monthly censuses by live trapping, of an 80-acre area in 1939, 1940, and 1941. The numbers underwent irregular changes not closely correlated with season, as this rodent breeds throughout most of the year with the fastest rate in spring. In 1946 the population had decreased to one per acre. Counts of those on roads at night and those dead on small plots where poison had been distributed indicated a population during 1935-1937 several times higher than the 1939-1941 maximum. Thus, large and unpredictable changes in its population density occur from year to year. Of the two species of pocket mice (*Perognathus*) the larger (*P. californicus*) is relatively scarce, the smaller (*P. inornatus*) was estimated to occur in densities of somewhat over three per acre in the summer of 1940. This was based on live trapping and marking on an 80-acre sampling area. This pocket mouse hibernates during the cold months and probably breeds several times in the dry season. Because of its minute size it is an important food source to newborn or newly hatched snakes. Three native cricetid "mouse" species of the genus *Peromyscus* (*maniculatus, boylii,* and *truei*) each occur in populations of from less than one per acre to, occasionally, several per acre. The meadow mouse (*Microtus californicus*) and harvest mouse (*Reithrodontomys megalotis*) are mainly restricted to some of the larger swales. The Merriam chipmunk (*Eutamias merriami*) is a brush-

land species, uncommon in this locality. The gray squirrel is at times moderately common but is not known to be preyed upon by any of the snake species. The house mouse is, so far as known, restricted to the vicinity of buildings, perhaps by unfavorable climate and abundance of native competitors.

Of the lizards, the skink (*Eumeces gilberti*) is much in evidence in the grass in rocky places in late March, April, and early May, but disappears during the dry season along with several other kinds of reptiles. Whether it becomes inactive, subterranean, or nocturnal remains an unsolved problem. The whiptail (*Cnemidophorus tessellatus*) is almost equally abundant and remains active throughout the summer. The fence lizard (*Sceloporus occidentalis*) is here a rock-dwelling species abundant wherever granite outcrops occur, and is active even throughout the winter whenever there is sunshine. The horned toad (*Phrynosoma coronatum*) is moderately common in grassy areas but was not recorded as prey of any snake, nor was the relatively scarce alligator lizard (*Gerrhonotus multicarinatus*). The brown-shouldered lizard (*Uta stansburiana*) is exceedingly abundant, doubtlessly attaining a population of several or many per acre on the drier and more open parts of the Range. Of amphibians, the California toad (*Bufo boreas*), tree-toad (*Hyla regilla*) and spadefoot toad (*Scaphiopus hammondii*) are all common, but probably the latter is most generally distributed. Its rapid development permits it to utilize ephemeral creeks and pools during the spring breeding season. The tiger salamander (*Ambystoma tigrinum*) and the introduced bullfrog (*Rana catesbeiana*) are limited to the vicinity of reservoirs in the headquarters area. The California red-legged frog (*Rana aurora*) has been observed only once on the area.

Every one of these prey species varied greatly in abundance from one part of the Range to another, according to the distribution and extent of preferred habitat — grassland, brush, rocks, trees or water. Though these rodent, lizard, and amphibian species make up nearly all the food of snakes at this locality, three bird species have been recorded among the prey, the quail (*Lophortyx californica*), oriole (*Icterus bullocki*) and towhee (*Pipilo fuscus*). The quail is a resident species that occurs in populations of .25 to .5 bird per acre (Glading, 1941: 35).

RATTLESNAKE

The local population of the widely distributed rattlesnake (*Crotalus viridis oreganus*) deviates from typical *oreganus* of coastal and more northern regions, in the direction of the Great Basin race *lutosus*, at least in color pattern. That habitat conditions approach the optimum for it in the area of the study is indicated not only by its high population, but by its large average and maximum size here. The largest specimen collected had an overall length of 53 inches, just under the 54-inch maximum for the subspecies recorded by Klauber (1937: 19) from many thousands of specimens from all parts of the geographic range.

A total of 679 rattlesnakes were recorded, marked, and released during the period April 1938 through April 1941, and data were recorded for 253 others killed during the same period or during the spring of 1946.

General behavior.—On unusually warm days in early spring an occasional rattlesnake is encountered before general emergence from hibernation has occurred. During the first period of mild weather, when daytime temperatures

are consistently above 70°F., there is a general emergence from hibernation. At this time the snakes are most often found in compact resting coils at the edges of rock outcrops, or in grass under dead brush. Often as many as three or four are found within a few square yards. The individuals of such small aggregations may be all of the same sex, or in pairs. At this time they are particularly sluggish, and often one will not move or rattle during the disturbance of catching or killing another only a few inches from it. All examined during the first few days after emergence were found to have empty stomachs.

For a period of weeks after emergence a large proportion of the adults are likely to be found in pairs. More than one-third of those taken in the spring of 1938, for example, were paired, indicating that mating either extends over a long time or occurs frequently. Sometimes the members of a pair were found coiled near together. On many other occasions actual courtship was seen, the male moving over the female with animated, jerky movements. Pairs were usually in well concealed situations, such as burrow entrances, or rock crevices, or under the edges of brush or logs. They were sensitive to disturbance, and quick to separate. In 1938, pairs were found over a 54-day period, in 1939 over a 36-day period and in 1940 over a 54-day period. Judging from these records the duration of the breeding season is about eight weeks.

For the first few weeks after emergence, while nights are still chilly, activity is strictly diurnal. However, the snakes often spend cold nights in the open as on many occasions they have been found early in the morning, coiled and sluggish, in vegetation matted down beneath them and wet with dew.

After a week or two of mild spring weather the snakes are more often found on the move, away from the immediate vicinity of shelter, and some of those found contain food. It is at this season that they are most frequently encountered by workers on the Range, and constitute a hazard. As weather becomes warmer, with high sunshine temperatures, snakes are less likely to be found in exposed situations, but may prowl through rocks, brush, and high grass.

In late spring, when the annual vegetation is drying out, and hot weather has set in, they are mainly crepuscular and nocturnal. At this season most of the snakes caught were located by the behavior and scolding chirps of ground squirrels. The squirrels forage actively in late afternoon and early evening, and their extensive burrow systems seem to provide the favorite shelter and prowling areas of the snakes, leading to frequent encounters. At this season also, the active squirrel population reaches its annual peak in numbers, with a high proportion of small young, of a size suitable to be eaten by the snakes. The peculiar chirp of a squirrel scolding a snake is characteristic, and at close range, unmistakable, and is accompanied by a nervous, jerky, sideways waving of the squirrel's tail. On many occasions squirrels not heard to chirp, but displaying the peculiar tail waving, were found to be watching rattlesnakes. So common are such encounters, that often several squirrels could be heard simultaneously, at different points, each scolding a snake. But locating such snakes was difficult because of the warning, sharp, alarm chirps of other squirrels at each move of the observer. These usually distracted and frightened away the ones which had been scolding before their exact whereabouts could be determined. Yet some squirrels were so intent upon snakes, that they could be approached

within a few yards. Even when a squirrel was sighted scolding and harrassing the snake from a few feet, it sometimes took many minutes of searching before the snake could be seen. Usually it was lying motionless and blending with its background. Such difficulty in detecting snakes whose presence and approximate position had already been betrayed, emphasized the efficiency of the concealing pattern. It also suggested the probability that for each one discovered in the field many were missed by field workers who may have walked near or even over them.

Upon discovery, snakes, either coiled or actively prowling in exposed places, often lay motionless and did not rattle. One found prowling on a bare swale bottom even allowed a person to stamp heavily just beside its head without making any movement. When actually touched, such snakes tried vigorously to escape, sometimes without rattling or showing fight, and sometimes backing away and rattling with forebody raised threateningly in a loop ready to strike. Unquestionably temperature and other environmental factors have an important effect on behavior, but individuality is likewise important. Unusually aggressive or unusually phlegmatic behavior noted at the time of capture and handling was generally borne out by subsequent captures of the same snake under different circumstances. An occasional snake encountered was so aggressive that it would become enraged at the mere presence of a person, and would advance menacingly, rattling and striking, even though such an advance took it away from the nearest shelter. Most lack such aggressiveness, and will not even rattle until actually touched; those that do so may either make for shelter or coil. Use of the rattle must constitute a decided detriment to those that encounter human beings, as it often leads to their destruction. Insofar as man's direct influence controls their populations, there is selection to eliminate the snakes that use their rattles.

A common defense reaction is the emission of anal scent from glands at the base of the tail by a frightened rattlesnake. The snake is capable of projecting this fluid in a spray of fine droplets for a distance of several feet, in a manner similar to that of a skunk. On numerous occasions in grasping an escaping rattlesnake by the tail or rattle to extricate it from some hole or crevice, the writer has been sprayed in the face, or even in the eyes. The secretion is without harmful effect, though it has a slightly disagreeable odor.

Prey is obtained by various methods, perhaps most frequently by coiling or lying in a strategic location, as in or beside rodent trails or burrows, and striking any animals that come within range. Active prowling is frequent also. Often on warm evenings, snakes recently emerged from shelter have been seen crawling slowly about ground squirrel burrow systems. Squirrels are apt to come unexpectedly upon such snakes in the course of their feeding, chasing and playing. A rattlesnake watched prowling slowly and circuitously over a dry and bare swale bottom evinced interest in fresh gopher mounds, and pressed its snout into the soil as if trying to force its way into the burrows. During the dry season, rodent burrows, especially those of ground squirrels, provide the usual daytime retreats. Often snakes have been seen emerging from them at dusk or shortly before. Sometimes in the late afternoon of hot summer days snakes have been seen inside holes, several inches from the entrances, apparently awaiting lower temperatures to emerge. The adult females in par-

ticular, may stay underground for long periods. Prey is perhaps often secured, eaten, and digested underground.

Composition of the population.—A sample of 1010 records of rattlesnakes based on 932 individuals marked and released or killed, and 78 recaptured after intervals including one or more periods of hibernation shows the relative numbers of different sizes encountered in the course of year-round field work. In such a sample, young may be represented in relatively large numbers because adults are more secretive or nocturnal except during a few weeks in spring following emergence from hibernation.

The length measurements upon which the following table, and other figures and discussions in this paper are based, pertain to the head-and-body-length only — the distance from the tip of the snout to the posterior edge of the anal plate. The head-and-body-length is the best basis for size comparisons because tail length is subject to sexual variation, and the rattle is often not perfect in adults.

The largest size groups are small young of the year between 301 and 450 mm.; full grown females with some subadult males between 751 and 850 mm.; and old adult males from 901 to 1100 mm.

TABLE 1.—Sizes of rattlesnakes in a year-round sample.

Head-and-body-length in mm.	Number of snakes	Head-and-body-length in mm.	Number of snakes
251-300	35	701- 750	59
301-350	88	751- 800	80
351-400	100	801- 850	100
401-450	74	851- 900	53
451-500	49	901- 950 and 951-1000	117
501-550	35	1001-1050 and 1051-1100	93
551-600	27	1101-1150 and 1151-1200	28
601-650	32	1201-1250 and 1251-1300	5
651-700	35		

A better index to the composition of the population may be obtained in spring when secretiveness and inactivity of certain sex and age groups are minimized. Records of 702 individuals are at hand for this period, as arbitrarily limited to the ten weeks after general emergence from hibernation in five different years, 1938, 1939, 1940, 1941, and 1946. The numbers in different size classes are shown in Table 2.

Snakes of this spring sample recorded in Table 2 illustrate that males are found in greater numbers than females, even in the small and half-grown snakes. Also, they bring out the fact that small young are much more numerous than those in later stages of growth, indicating heavy mortality during the first year. These points are further clarified by a regrouping of the records according to probable age as in Table 3.

The high ratio of males to females may be more apparent than actual.

Greater activity and larger individual ranges in the male snakes may cause them to be found in larger numbers. Other lines of evidence, as set forth in the section on "Numbers," suggest that actually the females may slightly outnumber the males.

Seasonal schedules of activity differ somewhat according to the age and sex of the individuals. During every month of the year that rattlesnakes were collected, the ratio of sex and size groups within the sample changed. Graphs (Figures 2 and 3) illustrating seasonal occurrence are based on the three year average for 1938, 1939, and 1940, as during each of these years time spent in the field from month to month was fairly constant. The same dates in different years are not strictly comparable. The spring of 1938 was cold with late rains so that rattlesnake emergence from hibernation, and onset of the breeding season were delayed five weeks as compared with beginning activity in the early spring of 1939. In 1940 conditions were intermediate between these extremes.

Ordinarily in this region no rattlesnakes are to be seen during the winter months, from some time in October until perhaps mid-March, or even in April.

TABLE 2.—Sizes of rattlesnakes in a spring sample.

Head-and-body-length in mm.	Number of snakes		Head-and-body-length in mm.	Number of snakes	
	Males	Females		Males	Females
251-300	11	15	701- 750	14	26
301-350	40	36	751- 800	18	47
351-400	38	18	801- 850	32	62
401-450	10	9	851- 900	21	23
451-500	6	6	901- 950 and 951-1000	78	5
501-550	14	12	1001-1050 and 1051-1100	70	1
551-600	9	12	1101-1150 and 1151-1200	15	0
601-650	9	16	1201-1250 and 1251-1300	4	0
651-700	13	12	Totals	402	300

TABLE 3.—Spring sample of 702 rattlesnakes showing relative numbers and sex ratios in age-size groups.

Probable age class	Percentage of total number	Size range (head-and-body-length in mm.)	Sex ratio males to females
First year young	22.5	251 to 400	1.29
Mainly young in second year	9.4	401 to 600 (males) 401 to 550 (females)	1.44
Mainly young in third (and fourth ?) years	13.4	601 to 800 (males) 551 to 700 (females)	1.35
Adults and subadults	54.7	801 to 1300 (males) 701 to 1100 (females)	1.40

The times of entrance into and emergence from hibernation depend on weather conditions.

For the purpose of demonstrating seasonal difference in abundance between young and adults, the entire lot has been divided into two groups — those less than 750 mm. in head and body length and those of 750 mm. or more (Figures 2 and 3). It is apparent that the adult snakes reach the peak of their abundance in April, and that their numbers dwindle rapidly in May and June, while the young snakes do not reach maximum numbers until May, and then dwindle more gradually through the dry season.

Within the adult group, male snakes reach a peak of abundance earlier than females, and in the latter part of the dry season apparently undergo a resurgence of activity, during August and September. The females reach the

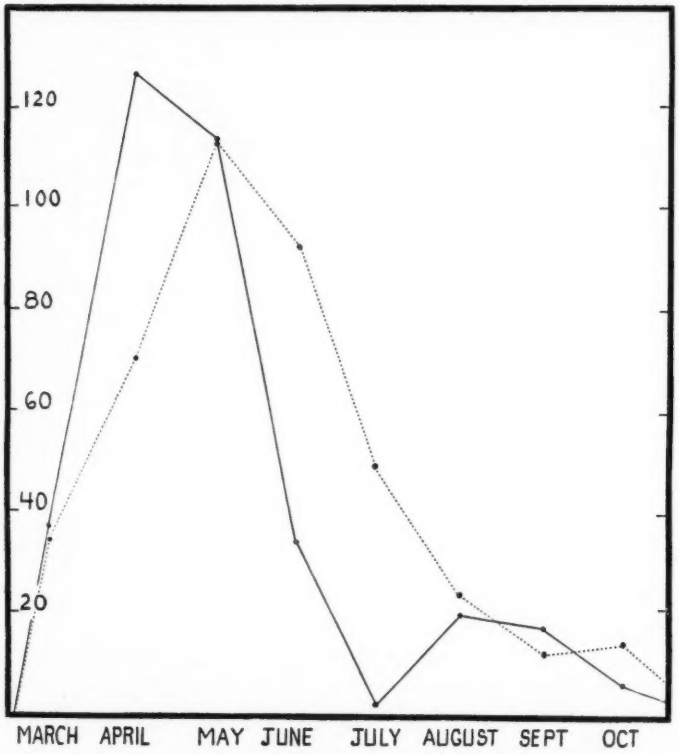

Fig. 2.—Seasonal occurrence by months, as indicated by the numbers killed or captured, of adult and subadult rattlesnakes—all those with head-and-body-lengths more than 750 mm. (solid line)—of young, head-and-body length less than 750 mm. (dotted line).

peak of their abundance in early May and taper off abruptly in June and July, being, mysteriously, almost entirely absent from the records during the dry season. Dwindling numbers in the young, at least, are due to change from diurnal to crepuscular and nocturnal prowling at the season when daytime temperatures are intolerably high in the open. Those taken during July and August were nearly all found at about sunset or later, and were usually seen as they emerged from rodent burrows. The adult snakes may have similar habits but with a tendency to emerge later at night, so that few are found. Evidence of this was obtained during the summer of 1946 when three adults (two of them females) and two young were kept and fed in a large outdoor pit simulating natural surroundings, with an insulated box for shelter. On hot days, all were invariably under cover, and the adults were rarely seen at all in the daytime, but the young were often out in the morning or evening, or any time when temperature was not too high. The adults sometimes emerged about dark, and in a series of observations made at various times during the first half of the night on different dates, one or more of the adults was usually out prowling.

Weight.—The weights of individual snakes were found to fluctuate in an irregular and unpredictable manner. Some apparently lost weight as a result

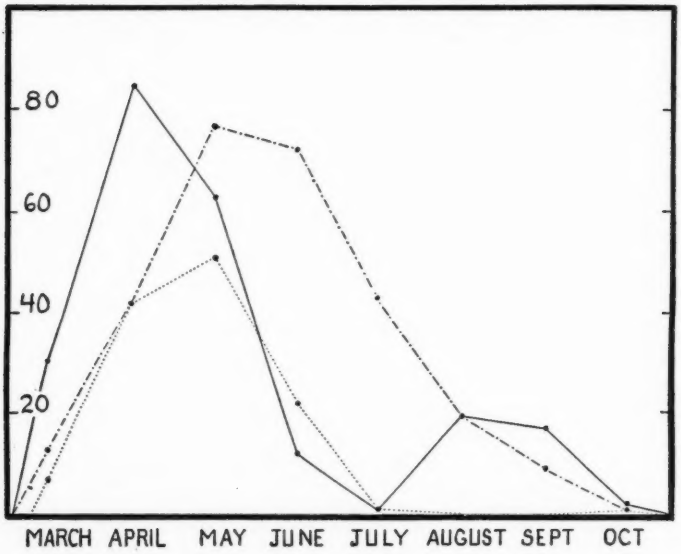

Fig. 3.—Seasonal occurrence of rattlesnakes: adult males (solid line), showing relative abundance in spring, and scarcity in midsummer; adult females (dotted line), showing virtual disappearance in late summer and fall; young (broken line, those with head-and-body-lengths less than 500 mm.) showing occurrence throughout the growing season in decreasing numbers (newborn young appearing in fall not included).

of handling. In a group of seven young (300-400 mm.) each recaptured after an interval of three to four weeks, six lost weight and the remaining one had made only insignificant gain. For the entire group the change amounted to an average loss of 18.8 percent of the original weight. The greatest relative decrease was 39 percent from 29½ to 18 grams.

For seven young of the same size group recaptured after four to six weeks, weight changes amounted to an average loss of 3.4 percent; four had lost, two had gained, and one weighed the same. For sixteen young recaptured after intervals from 1½ to 3 months, three had lost, one weighed the same, and twelve had gained amounts up to 81 percent; the average change amounted to a gain of 28.5 percent. Of thirteen young recaptured after 3 to 10 months, two had lost weight and eleven had gained; the average change was a 39.4 percent increase. The greatest gain amounted to 186 percent. It is doubtful whether any deleterious effects from handling would have persisted this long. For six recaptured after intervals of 10 to 13 months, there was an average weight gain of 69.7 percent; but two lost weight, 17.1 and 25.4 percent, respectively. One recaptured after not quite 13 months had lost 44.5 percent; another after 16 months had lost 9.5 percent. The remaining young were recaptured after intervals of from 14 to 92 months and had gained from 88.7 to 900.0 percent of the original weight. Weight changes in adults and subadults were likewise unpredictable with varying losses and gains. In Table 4 the sexes in adults are listed separately; carrying of young throughout most of the growing season by females, and their lesser activity causes them to deviate markedly from the male pattern.

While weight gains depend upon the quantity eaten, losses are determined largely by the humidity and temperature. In the rodent burrows, where the snakes spend most of their time in hot weather, temperatures are lower and humidities higher than on the soil surface, favoring maintenance of body weight. Those snakes spending part of the time prowling in the open probably lose weight most rapidly.

As an example of progressive deterioration (probably due, in part at least, to the deleterious effects of handling) a young female (440 mm.) captured six times at the same place within a two-month period, weighed:

Jul. 30	50.5 grams
Aug. 2	45.5 grams
Aug. 8	40.0 grams
Aug. 18	38.5 grams
Aug. 28	36.5 grams
Sep. 28	26.5 grams

Adult rattlesnakes in good condition have quantities of stored fat that may carry them over fasting periods, while young were observed to have no such reserve. During fasting periods, young lose weight much more rapidly in proportion to their own weight than adults do. Klauber (1937: 52) found that in Colorado prairie rattlesnakes of this species during hibernation, young lost over 20 per cent of their body weight but adults lost somewhat less than 4 percent. Losses would be much more rapid at high summer temperatures. The situation of the young is precarious as compared with that of adults, as

they must eat frequently or become emaciated and having once sustained a large weight loss, the chances of survival progressively deteriorate. In its weakened condition, the snake would be liable to fail in an attempt to secure prey or to swallow it, even when opportunity arose. Presence of abundant rodent or lizard populations of sufficiently small size to be swallowed by the smallest young must be an important ecological factor.

Weight at birth may average somewhat less than 20 grams (young were found weighing as little as 6 grams), while the largest adults weigh more than 1200 grams. Adult females, being smaller than males, are likely to weigh between 300 and 400 grams, usually not exceeding 500 (Fitch and Glading, 1947: 118).

TABLE 4.—Weight changes in recaptured rattlesnakes. (Plus and minus signs are used to indicate records within two weeks after or before the even month).

A. Young

Elapsed time of records in months	Original length in mm.	Original weight in grams	Percentage weight gain	Percentage weight loss	Elapsed time of records in months	Original length in mm.	Original weight in grams	Percentage weight gain	Percentage weight loss
1—	475	44½		25.8	3—	390	30½	60.6	
1—	422	44		15.9	3+	317	15½	29.0	
1—	359	29½		39.0	3+	350	23	8.7	
1—	398	40		17.5	4—	454	66½	3.8	
1—	447	51		10.8	4+	336	23	17.4	
1—	406	46		25.7	4+	536	104	92.3	
1—	366	31	3.2		5—	572	107		24.3
1+	342	21		1.0	8—	440	52½		23.0
1+	367	30½		16.4	8—	482	43	101.0	
1+	486	63½		12.6	8+	467	60½	17.4	
1+	363	31		11.3	9—	459	83½	12.6	
1+	322	16	none	none	9+	360	28	186.0	
1+	340	27	16.7		10—	286	18	12.8	
1+	394	43½	.5		10—	450	43½	79.3	
2—	440	50½		47.5	10+	551	120		25.4
2—	383	49		30.6	11—	321	20½	129.0	
2—	538	74½	29.5		11	510	82		17.1
2—	585	142	42.1		12—	373	24½	100.0	
2—	332	17½	60.0		12—	395	33½	44.8	
2—	516	68	44.1		12+	395	28	187.0	
2—	483	75	3.0		13—	361	36		44.5
2—	389	31	25.8		14+	385	33	176.0	
2	349	21	81.0		16	346	31½		9.5
2+	367	32	none	none	21+	561	107	88.7	
2+	293	17½	37.1		69—	463	51½	900.0	
2+	350	23½	46.8		74—	502	64	246.0	
3—	362	30		38.3	84—	438	40	725.0	
3—	433	17	76.4		92+	497	69	315.0	

TABLE 4.—Continued.

B. Adult and subadult males

Elapsed time of records in months	Original length in mm.	Original weight in grams	Percentage weight gain	Percentage weight loss	Elapsed time of records in months	Original length in mm.	Original weight in grams	Percentage weight gain	Percentage weight loss
1—	982	630	14.1		19—	1056	874	1.8	
1+	1038	662		4.0	22+	698	174	59.6	
2—	1015	857		.2	23+	691	269		9.7
2—	1000	629	.2		26—	1086	1123		27.0
2+	977	619	8.9		29+	890	490	16.1	
7+	1168	1153		5.6	37+	775	317	1.3	
7+	930	418	7.2		61—	1034	668	37.0	
7+	752	331		17.0	68—	971	626	62.4	
9—	830	350	13.1		68+	1028	825	6.1	
9+	908	785		28.0	71—	940	710	18.6	
10+	1090	706		8.3	71—	966	694	42.0	
12—	821	368		4.9	72—	1047	714	28.4	
12—	996	735		2.6	72—	985	538	46.0	
12	1124	1070		21.2	73—	612	125	129.0	
12	888	457	15.1		84	1000	680	29.9	
12	663	187	58.8		84	824	450	82.3	
14—	803	289	32.2		91	930	570	63.0	

C. Adult and subadult females

3—	818	279	32.6		71—	820	451		30.3
3+	1011	632		20.4	72—	789	245	17.1	
10+	865	570		34.2	83—	767	284		23.3
11+	890	417		18.5	84	763	322	20.2	
13—	850	548		23.6	85—	795	383		18.5
22—	720	272	15.8		94	840	327	16.2	

Weight fluctuations probably paralleling those under natural conditions were recorded in the three snakes kept through most of the 1946 growing season and the following winter in a large outdoor concrete pit. These snakes were not handled or measured before or during the experiment because of the apparently deleterious effects of such treatment. Records of each follow:

Number 1, *Adult female.*—Collected on April 22; had fed several days previously on large prey probably weighing more than 100 grams.

Apr. 22	Weight 491 grams	Aug. 15	Ate gopher 78 grams
Apr. 30	Ate young meadow mouse 7 grams	Aug. 20	Ate kangaroo rat 61 grams
May 13	Ate kangaroo rat 35 grams	Aug. 31	Ate gopher 94 grams
May 15	Ate brush mouse 23½ grams	Sep. 18	Weight 400 grams
Jul. 9	Shed skin	Nov. 30	Weight 350 grams (partly torpid)
Jul. 25	Ate gopher 59 grams	Dec. 29	Weight 350 grams (partly torpid)
Jul. 25	Weight 370 grams	Feb. 23	Weight 340 grams (partly torpid)
		Mar. 25	Weight 337 grams

Number 2, *Subadult male.*—Collected on April 25; appeared thin and probably had not fed since hibernation; found inside fenced enclosure from which rodents were removed during the preceding winter.

Apr. 25	Weight 164 grams		Jul. 31	Weight 270 grams	
May 12	Ate gopher	60 grams	Sep. 18	Weight 220 grams	
May 14	Ate kangaroo rat	46 grams	Nov. 30	Weight 191 grams	(partly torpid)
Jul. 10	Ate gopher	89 grams	Feb. 23	Weight 188 grams	(partly torpid)
Jul. 28	Ate kangaroo rat	63 grams	Mar. 25	Weight 185 grams	

Number 3, *Female.*—Collected on May 11; known to be 7½ years old, having been marked more than 6 years before as large juvenile.

May 11	Weight 226 grams		Sep. 18	Weight 230 grams	
May 13	Ate gopher	21 grams	Nov. 30	Weight 214 grams	(partly torpid)
May 23	Ate brush mouse	26 grams	Dec. 29	Weight 216 grams	(partly torpid)
Jul. 7	Ate kangaroo rat	52 grams	Feb. 23	Weight 210 grams	(partly torpid)
Jul. 31	Weight 220 grams		Mar. 25	Weight 209 grams	
Aug. 21	Ate gopher	105 grams			

A young rattlesnake kept with the adults survived for only part of the summer. Its weight changed as follows:

Collected on May 20; length 293 mm.

May 20 Weight 20 grams — Jul. 31 Weight 13½ grams

Rattles.—Like growth in length, rattle growth is unpredictable and subject to much variation. Young born in the fall have but a single rattle, the button, and only one of 18 taken soon after emergence in spring had acquired a second rattle. Many had not acquired a second rattle by the following June, but by late summer nearly all had added second and third rattles. Few year old snakes were in evidence during the fall, but upon emerging the following spring from their second hibernation, some still had only three rattles. Four is probably the most frequent number, while a few have five at that age and season.

Seasonal occurrence of young with various numbers of rattles was as shown in Table 5.

TABLE 5.—Young rattlesnakes classified according to month and rattle number.

Month	*Number of rattles*					
	1	*2*	*3*	*4*	*5*	*6*
March	18	1	4	10	6	7
April	38	1	8	9	6	5
May	36	33	6	12	7	7
June	11	47	12	8	7	5
July	1	12	27	3	2	1
August	0	4	24	5	5	3
September	2	0	5	6	1	2
October (and Nov.)	9	0	3	0	1	1

Young with only one rattle, the button, were, as shown above, collected in every month of the growing season except August, but occurred mainly just

before hibernation in the fall (when evidently all of them are born) and in the months following emergence from hibernation. The single July record (on the 6th) was in the unusually late season of 1938 and pertained to a retarded young one. Those with one rattle and a button were collected in every growing-month except September and October, but principally in May and June. The two taken in March and April had added the second rattle sooner than usual as result of early fall birth and rapid development, while a few retarded ones did not add third rattles until July or even August. Young with three rattles were taken in every month of the growing season but with a definite July-August peak indicating that the majority were in this stage at the age of nine or ten months. By the time this stage is reached, successive annual broods may overlap in rattle number, and cannot be identified with certainty. Such overlapping probably occurs mainly in early summer, say in June. Then the most vigorous young of the preceding fall brood add a third rattle at the age of eight or nine months, while retarded individuals born a year before have failed to gain their fourth rattle at an age of twenty months. Young having four, five, and six rattles were taken in every month of the growing season, and each group was found in greatest numbers during the months following hibernation, for the reason that rattlesnakes in general are more active and more diurnal then. However, the 4-rattle young were taken in slightly greater numbers than the 3-rattle young in this season, indicating that the transition from three to four rattles is most likely to take place shortly before the second hibernation, that is, at the age of about one year. Numbers of 5-rattle young most nearly approach those of 4-rattle young during July and August, indicating that the transition to the former condition most often takes place in early summer after the second hibernation, that is, at an age of roughly 19 or 20 months.

Grouped according to rattle number, those snakes having unbroken strings of rattles occurred in the following numbers: one rattle, 115; two rattles, 98; three rattles, 89; four rattles, 53; five rattles, 35; six rattles, 31; seven rattles, 44; eight rattles, 54; nine rattles, 34; ten rattles, 15; eleven rattles, 13. Snakes having strings of five and six rattles were comparatively scarce among those recorded because the majority of individuals pass through both stages during the late spring, summer and early fall months when they are nocturnal in habits, and less apt to be encountered. Rattle number in snakes with complete strings is perhaps a more accurate indicator of age than is size or length. However, most snakes lose the button and other early rattles before a long string is attained, through normal wear and breakage. In those snakes that have added a total of not more than nine or ten rattles, broken strings usually taper abruptly, but in old adults the terminal rattles are as wide as the basal ones.

The combined data from records of marked snakes recaptured, and from all young collected throughout the growing season and sorted into age-size-rattle classes, indicate the trend of rattle development. Young a little more than one year old and just entering their second hibernation most typically have strings of four rattles, and those entering their third hibernations probably most often have strings of six or even seven rattles. In adults, however, ecdyses, and resulting rattle gains occur less frequently than in growing young.

For the adult males listed in Table 7 below, a gain of one rattle per 4.7

growing-season-months, or an average of three rattles in two years is indicated. Contrasted with this figure, the rate of rattle growth in adult females is markedly lower. Eight females in a total combined time of 213 growing-season-months added a combined total of 33 rattles — one per 6.5 growing-season-months, or, on the average, 1.1 rattles annually. In this locality at least, it would seem that the adult females closely approximate the one-rattle annual gain of folklore and legend. Only one of the eight females deviated from this trend, by adding four rattles in 24 months.

TABLE 6.—Rattlesnakes grouped according to size and rattle number.

A. Young

Head-and-body-length in mm.	Number of rattles								
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
251- 300	30	2							
301- 350	69	12	1						
351- 400	15	60	22	1					
401- 450	1	22	41	5	1				
451- 500		2	22	28	3				
501- 550			3	15	11	1		1	
551- 600				10	8	7	1		
601- 650				4	8	10	5	4	
651- 700					4	5	12	5	4

B. Subadult and adult females

Head-and-body-length in mm.	Number of rattles									Some missing (tapered)	Some missing (not tapered)
	6	*7*	*8*	*9*	*10*	*11*	*12*	*13**	*17**		
701- 750	2	2	12	2						11	5
751- 800	2	10	3	8	2	3	1			13	13
801- 850		1	3	4	2	1		2	1	11	39
851- 900		2	1	1	1					9	19
901-1000						2				1	6
1001-1100											1

* From recorded gains of marked snakes originally having complete strings.

TABLE 6.—Continued.

C. Subadult and adult males

Head-and-body-length in mm.	Number of rattles										Some missing (tapered)	Some missing (not tapered)
	5	6	7	8	9	10	11	12	13	14		
701- 750	1	6	4	4	1							1
751- 800			6	8	2	1		1			5	2
801- 850			1	9	5	3					9	8
851- 900				3	1	3	2				3	9
901-1000				1	6	3	4	1	2		22	68
1001-1100							1	1		1	10	78
1101-1200												28
1201-1300												5

In Table 7 the "Number of months between captures" column shows both the total months elapsed and (in parentheses) the months of growing season exclusive of hibernation for each individual — allowing a probable five-months hibernation period each year.

In comparatively few instances were rattle gains known in snakes that were marked either as young or as adults, and recaptured after long periods of years. Many of those recaptured after long periods had lost their marked rattle segments, and hence may have grown and lost one or several besides the string actually counted at the time of recapture. The few in which the marked segments remained are of exceptional interest in revealing the average gain to be expected, particularly as any handicap resulting from handling would be minimized after so long a time. Those snakes retaining the marked rattles after periods of years were possibly the slowest developing, and therefore might not be entirely representative of the average rate of gain.

Two adult males were known to have gained 9 and 8 rattles in just under 68 and 72 months respectively, and they averaged a gain of one rattle to 4.7 growing-season-months, almost exactly the same average gain recorded for males recaptured after shorter intervals. Eleven of fourteen other adult males completely replaced their rattle strings, including, in each, the wired rattle (with an average of 8.4 segments to a string) in five to eight year periods. Some probably grew several more rattles than actually recorded, and they might slightly increase the adult male rate of rattle replacement, of 1.5 rattle segments annually, if their records were complete.

Of seven adult females recaptured at 71 to 94 months after marking, four retained the marked rattles, and each had made a consistent gain of one rattle annually. The three that did not retain the marked rattle had comparatively short stubs as their rattle strings, with only four, five, and five segments re-

spectively. There is no indication from these long time records that females ordinarily gain more than one rattle in a year. One of the three females that did not retain a marked rattle 94 months from its original marking, was known to have gained three segments during the first three years, evidently conforming with the usual pattern.

TABLE 7.—Rattle gains in recaptured rattlesnakes.

A. Adult males

No. of months elapsed between captures	Original rattle number	Rattle gain	No. of months elapsed between captures	Original rattle number	Rattle gain
1—	incomplete	0	12— (7—)	incomplete	1
1+	incomplete	0	12 (7)	incomplete	1
2—	incomplete	0	12 (7)	11	2
2—	incomplete	1	14— (9—)	8	2
2+	incomplete	1	19— (9—)	incomplete	2
3+	incomplete	1 (at least)	24+ (14+)	incomplete	2
6—	incomplete	2	24+ (14+)	incomplete	4
7+ (2+)	incomplete	1	26— (16—)	incomplete	3
7+ (2+)	11	1	29+ (14+)	incomplete	3
7+ (2+)	incomplete	1	37+ (22+)	7	3
9— (4—)	7	1	68— (38—)	incomplete	9
9— (4—)	9	0	72— (42—)	incomplete	8
10+ (5+)	incomplete	1			

B. Adult females

3—	incomplete	1 (at least)	71+ (41+)	9	6
11+ (7+)	incomplete	1	83— (48—)	9	7
13— (8—)	8	1	84 (49)	6	7
24+ (14+)	incomplete	4	85— (50—)	11	6

For snakes marked as young and recaptured as adults records of rattle gain are meager. The outstanding example is that of a female marked at a length of 497 mm. when it had two rattles and a button, in August 1938. A juvenile of this size and rattle number in late summer must almost certainly have been born the preceding fall, say in October, 1937, so its career may be traced from birth to the time of its final capture in April 1946 at an age of eight years and six months. It then had a string of thirteen rattles, including the button which was partly broken away. If it acquired its seventh rattle after emerging from its third hibernation, and added one rattle annually thereafter, it conformed closely with the pattern tentatively pieced together from records of numerous individuals over shorter periods. A less conclusive record involved a female marked at a length of 502 mm., with three rattles and a button, in March 1940. Probably this was soon after its emergence from its second hibernation at an age of 17 months. It was recaptured 74 months later, in May, 1946. Then, at a probable age of 7½ years, it had a head-and-body-

length of 660 mm., still several inches short of adult female size, and it had a broken but tapering string of four rattles. From comparison with other rattle strings, it was estimated that five had been lost, including the button, and if this estimate is correct, it had added only five rattles in more than six years.

A male was marked in August 1940, at a probable age of ten months. It was 463 mm. long, with two rattles and a button. Nearly 69 months later it was recaptured as an adult, having virtually doubled in length to 925 mm. and having an incomplete but tapering string of eight rattles. Comparison of these segments with those of other strings indicated that the number missing was probably either four or five. At an age of six years and seven months this snake had grown to the size of a medium-small adult, and evidently had grown a total of 12 or 13 rattles. A male marked in April when it had only a button, was recaptured six years and two months later and had added ten rattles. It was still hardly more than half-grown size (evidently stunted by an injury). Several of its basal rattles were of uniform width.

Growth.—Growth was investigated by recording the gains of marked rattlesnakes recaptured, and by sorting all young taken into probable age groups on the basis of their sizes and rattle numbers. Even with these combined methods, the course of growth beyond the first year is obscure. Successive annual classes begin to overlap in size and rattle numbers, and average growth shown by recaptured individuals cannot be accepted as typical; many of them are stunted.

The stunting which results from handling and marking has already been mentioned under the section on "Weight," where it was shown that the recovery is apt to take more than a month. Food palped from snakes was always forced back into their stomachs, and usually the snakes cooperated with active swallowing movements, rather than resisting. In only a few instances was such prey disgorged after release of the snake. Muscular or skeletal injuries may have been sustained by the snakes held down and stretched for measurement. Struggles to escape or retaliate sometimes resulted in lost venom, or even bruised mouths or broken fangs, although effort was made to avoid such handicaps. As a result of the injuries and disturbance involved in handling and marking, snakes are evidently disinclined to feed normally after their release.

Also, even under normal conditions, many of the less vigorous young are probably eliminated by starvation. Inclusion of the records of such individuals to compute the "average" growth rate will lead to an erroneous impression of the time required to reach adult size. There is perhaps a greater likelihood of catching those snakes that are unsuccessful in obtaining prey, as they may spend more time prowling.

Average growth rate recorded in young snakes marked and recaptured was remarkably slow for these reasons, as compared with that of unhandicapped individuals of known age. In young measured in early spring, and recognizable from their sizes and rattle numbers as the survivors of two hibernations, average head-and-body-length approximated 500 mm. Hence, in about 19

months (10 of it spent in dormancy) since birth they had grown some 220 mm., an average increase in length of about 24 mm. for each month of active life. The majority of the young marked and recaptured failed to maintain this rapid growth rate during the interval between captures, and thus evidenced varying degrees of stunting as a direct result of handling. In a series of 31 such young recaptured, the ten that grew most rapidly maintained, as a group, an approximately normal growth rate. The remaining 21, just over two-thirds of the entire group, fell far behind.

Individual differences in rate of development result in such divergence that in their second summer the young apparently overlap widely those of younger and older age classes in both size and rattle number. Therefore they no longer can be identified as a group and their growth cannot be traced directly. Their growth cannot be measured directly by records of recaptures, either, because of the stunting factor. But by assuming that handling causes about the same degree of stunting in these half-grown snakes as in smaller ones, the growth curve may be projected through the second growing season, and beyond. For the purpose of comparing rates of growth and rattle development in the recaptured half-grown snakes with that in recaptured smaller ones, each size class has been divided into three approximately equal groups — those with

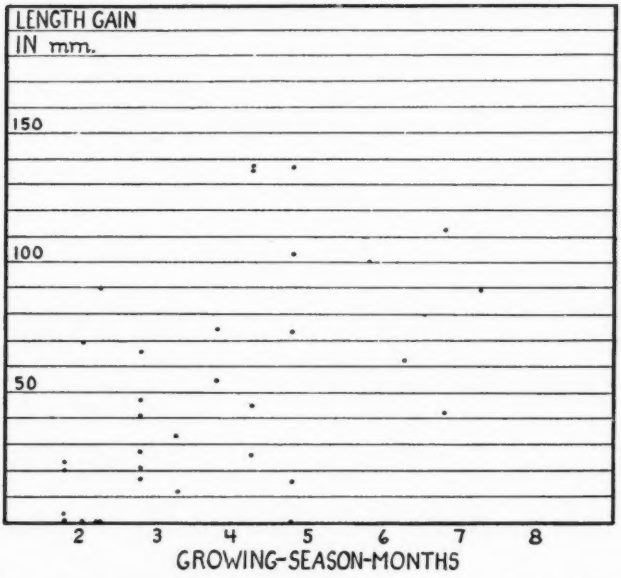

Fig. 4.—Length gains (head-and-body) in recaptured young rattlesnakes (those with head-and-body-length less than 500 mm.), showing the extreme differences between individuals in rate of growth.

fastest growth, regarded as normal, those somewhat stunted, and those most stunted, as shown in Table 8.

These records show that individuals differ a great deal in their rates of growth and of rattle development. Also they show that individuals stunted in growth tend to gain rattles much more slowly than do those making normal growth.

The records of a group of 22 larger young marked and recaptured seem to represent mainly development in the second growing season, though some were obviously less than a year old when marked, and several others probably were more than two years old. These are shown in Table 9.

A comparison between the first year and well grown young, of fast, medium and slow growth groups, as shown in Table 10, brings out differences in rate of length gains and rattle gains. Monthly length increments decrease only slightly during the second growing season, but frequency of rattle gains falls

TABLE 8.—Individual records of first-year young rattlesnakes marked and recaptured.

Sex	Months elapsed between captures (probable months of dormancy in parentheses)	Head-and-body-length in mm.	Rattle number including button	Sex	Months elapsed between captures (probable months of dormancy in parentheses)	Head-and-body-length in mm.	Rattle number including button
A. Fast Group (Normal)							
♂	1	397 to 465	2 to 3	♀	4—	454 to 528	2 to 4
♂	2+	293 to 383	1 to 2	♀	3—	390 to 437	2 to 3
♀	1—	340 to 368	1 to 2	♀	12— (5)	373 to 485	2 to 4
♂	2	349 to 418	2 to 3	♀	8— (5)	482 to 523	3 to 4
♂	9+ (5)	360 to 497	2 to 4	♀	11— (5)	321 to 421	3 to 4
B. Medium Group (Somewhat stunted)							
♂	14 (5)	385 to 520	2 to 5	♀	3+	350 to 383	2 to 3
♂	10— (5)	286 to 359	1 to 3	♂	21— (10)	450 to 553	3 to 4
♂	1+	394 to 411	2 to 3	♂	12— (5)	395 to 437	1 to 2
♀	2—	332 to 355	1 to 2	♂	3—	317 to 338	1 to 2
♀	12+ (5)	395 to 484	2 to 3	♂	11+ (5)	383 to 445	2 to 3
C. Slow Group (Much stunted)							
♀	3—	433 to 450	3 to 4	♂	13— (5)	361 to 362	1 to 3
♂	4+	336 to 362	1 to 3	♂	6 (5)	500 to 500	3 to 3
♀	10— (5)	413 to 429	2 to 3	♂	2+	367 to 367	2 to 2
♂	3—	362 to 369	2 to 3	♀	2+	350 to 350	2 to 3
♂	8+ (5)	467 to 479	3 to 4	♂	1—	359 to 359	2 to 3
♂	16+ (5)	346 to 373	1 to 3				

TABLE 9.—Individual records of well-grown young rattlesnakes marked and recaptured.

Sex	Months elapsed between captures (probable months of dormancy in parentheses)	Head-and-body-length in mm.	Rattle number (including button except where marked with asterisk)
A. Fast Group (Normal ?)			
♂	22+ (10)	365 to 762	2 to 8
♂	4+	536 to 657	4 to 6
♂	2—	585 to 633	5 to 5
♂	12 (5)	663 to 805	7 to 9
♀	27— (10)	310 to 623	1 to ?
♂	23+ (10)	443 to 650	3 to 7
♂	11+ (5)	543 to 630	5 to 6
B. Medium Group (Somewhat stunted)			
♂	12— (5)	695 to 795	6 to ?
♀	9— (5)	459 to 513	3 to 5
♂	21+ (10)	561 to 695	5 to 8
♂	24+ (10)	720 to 860	7*to 8*
♀	2—	516 to 530	4 to 5
♀	22+ (10)	590 to 690	5 to 7
♀	36 (15)	590 to 727	5 to 8
♂	2—	538 to 550	5 to 5
C. Slow Group (Much stunted)			
♂	22+ (10)	698 to 757	6 to 8
♂	11 (5)	510 to 538	1*to 2*
♀	13+ (5)	690 to 727	7 to 8
♂	23+ (10)	691 to 713	6 to 8
♂	10+ (5)	551 to 555	5 to 6
♀	5—	572 to 572	4 to 5
♂	7+ (5)	752 to 752	1 to 2

TABLE 10.—Comparison between first year young and well-grown young in rates of length gains and rattle gains.

	Average head-and-body-length gain per month, in mm.		Average time, in growing-season-months, elapsed between each rattle gain	
	First year young	Well grown young	First year young	Well grown young
Fast group	24.0	21.9	2.46	3.28
Medium group	10.9	11.0	4.14	4.67
Slow group	2.2	2.9	4.00	5.75

off abruptly. Whereas in the first year young, intervals of only about 2½ months intervene between ecdyses, these intervals have lengthened to 3¼ months in the well-grown young.

According to the growth rate inferred from these figures, a snake 500 mm. long at the time of entering its second hibernation would be about 650 mm. long a year later, and would reach 800 mm. at the end of another year — when slightly over three years old, if it continued to grow at this same rate.

Probably growth continues to slow down as adult size is approached. This is indicated by the ten "subadult" snakes ranging from 663 to 890 mm., which were marked and recaptured after substantial intervals, but which were still short of full adult size. The sample is, of course, inadequate, but the data show average length gains for the fast, medium and slow groups of 16.3, 6.5, and 1.2 mm., respectively. By the time a snake attained a length of 900 mm. it would ordinarily be more than four years old.

Continued growth after attainment of adult size occurred in some individ-

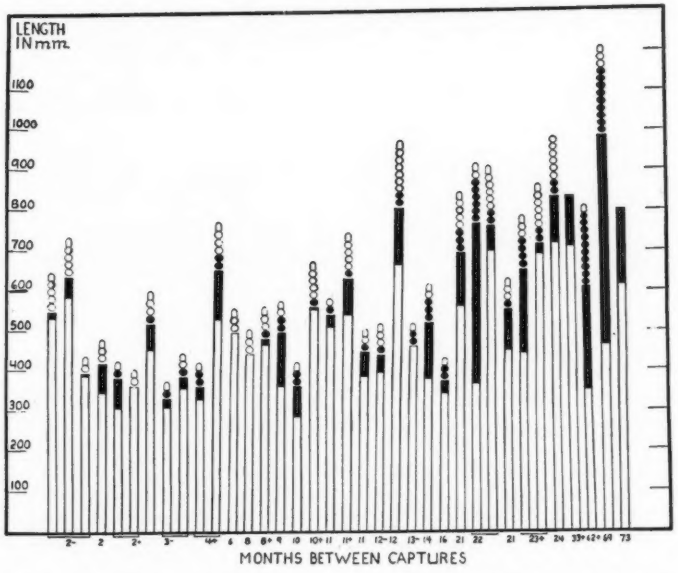

Fig. 5.—Growth and rattle development in young male rattlesnakes. Each column represents an individual snake recaptured one or more times; open portion shows head-and-body-length at original capture, solid portion shows gain between captures. Open circles represent rattles present at original capture, with the "button" shown where present, and solid circles represent recorded rattle gains. Records from 1947 are not included; otherwise all those recorded after intervals longer than six weeks are shown.

uals recaptured after periods of years, but others of similar sizes failed to make measurable growth. Most of the records of growth in adults pertained to individuals which had tapering rattle strings at the time of marking, showing them to be relatively young. Females of adult size tended to grow less than males and were more often completely static. Some of the more clear cut records of growth in snakes already near, or well above small adult size are as follows.

Nine year interval: ♂, 860 to 998 mm., rattles originally 8 (complete).

Eight year interval: ♂, 834 to 1072 mm.; ♂, 930 to 1075 mm., rattles originally 10 (complete), 570 to 928 gms.; ♂, 551 to 849 mm., rattles originally 5 (complete), 120 to 540 gms.; ♀, 735 to 766 mm., rattles originally 8, 221 to 270 gms.; ♀, 840 to 870 mm., rattles originally 6 (incomplete, not tapered).

Seven year interval: ♂, 824 to 938 mm., rattles originally 10, 9 more added, 450 to 820 gms.; ♀, 763 to 840 mm., rattles originally 6 (complete), 7 more added, 322 to 387 gms.

Six year interval: ♂, 940 to 1043 mm., rattles originally 13 (complete), 710 to 842 gms.; ♂, 966 to 1038 mm., rattles originally 7 (incomplete, not tapered), 694 to 985 gms.; ♂, 971 to 1088 mm., rattles originally 8 (incomplete, not tapered), 9 more added, 626 to 1017 gms.; ♂, 612 to 799 mm., rattles originally 7 (complete), 4 or 5 more added (estimate, end broken off), 125 to 285 gms.

Several adults were recorded to be exactly the same lengths after periods of years, as follows: eight year interval, ♂, 942 mm., rattles originally 7 (incomplete, not tapered), 640 to 505 gms.; seven year interval, ♀, 767 mm., rattles originally 9 (complete), 7 more added, 284 to 276 gms.; six year interval: ♀, 880 mm., rattles originally 9 (complete), 6 more added, 275 to 310 gms.; ♀, 820 mm., rattles originally 4 (incomplete, not tapered), weight 451 to 314 gms.

Snakes classed as old adults at the time of marking, on the basis of their size and rattles, and recaptured after five to eight year intervals, increased over their original lengths by the following percentages. For males: 12.0, 9.3, 9.2, 6.3, 5.1, 4.2, 3.9, none, and none; for females: 4.7, 3.6, none. Of those classed as subadults at the time of marking, two females, each having complete strings of nine rattles, made no length gain while other females gained 10.0, 4.1, and 2.0 percent respectively. The subadult males made gains of 30.4, 25.5, 16.0, 15.6, 13.8, and 11.0 percent. In general it appears that females, once having attained adult size, are much less inclined to continued gradual growth than are males.

It will be apparent that no stereotyped growth pattern exists in this species but that each individual develops at its own rate, determined by success in obtaining food, natural vigor, and probably by many other environmental factors. However, the rate of development indicated in Table 11 is perhaps most typical, for this locality at least.

TABLE 11.—Chronology and correlation of rattle number, head-and-body-length and age in typical development of a rattlesnake at San Joaquin Experimental Range.

Number of rattles	Head-and-body-length in mm.	Month	Age in months
"Prebutton"	280	October	Birth
1	315	April	6— (5 in hibernation)
2	375	June	8 (5 in hibernation)
3	435	August	10½ (5 in hibernation)
4	500	April	18 (10 in hibernation)
5	565	July	21 (10 in hibernation)
6	630	October	24 (10 in hibernation)
7	680	June	32 (15 in hibernation)
8	720	September	35 (15 in hibernation)

Fig. 6.—Young female rattlesnake that from May 20, 1938 to August 13, 1940 doubled in length—310 to 623 mm.

In young having as many as eight rattles, the males average at least 50 mm. longer than the females, as there is disparity between the sexes in adult size. For young rattlesnakes having complete strings of rattles (i.e. including the original button) the average head-and-body-length increased for each successive segment. However, for each rattle number the head-and-body-length range recorded was remarkable. Some snakes having three rattles were no larger than the spring average of those having only one. Of those having five rattles the smallest (423 mm.) was exceeded in size by several having only two

rattles, while the largest (712 mm.) exceeded in size some having nine rattles. In each group there were some individuals which appeared stunted. Such individuals, having a high ratio of rattle number to length, often appeared emaciated also.

Longevity.—The nine-year span of the study was far too short to determine the potential longevity, but the age trends of those individuals recaptured after five to nine year intervals are significant. The 28 recaptured in 1946 and 1947, after an average interval of 77 months, included 12 that at the time of marking were old adults (with incomplete and untapered rattle strings), eight that were young adults or subadults (above the minimum adult size, with complete strings of nine or more rattles) and seven young. In the old adults, each with uniformly wide rattle segments, the number of segments averaged 7.8 in nine males and 5.7 in three females at the time of original capture. In each sex these strings represented an accumulation of five to six years' growth (one rattle per year in females and 1.5 per year in males). Hence, at the time of recapture, seven years later, this group must have averaged *a minimum* of 12 years as adults. Previous to this each must have spent about four years in growing to full adult size. Therefore, snakes of this group must have been at least 16 years of age at the time of recapture, and probably some of them were much older then. In view of these data, it seems probable that large adults with long strings of uniformly wide rattles are likely to be as much as 20 years old. Obviously the life span of a rattlesnake is much greater than that of its prey species. Also, it is likely to exceed that of associated predators of other types, such as coyotes, foxes, hawks, and owls.

Apparently life expectancy increases as larger size is attained, conferring increasing immunity to the dangers that beset the small young. Among the 679 rattlesnakes marked in 1938-1941, about 29 percent were old adults, but among those of this group recaptured in 1946-1947 the ones which were already old adults when marked comprised 43 percent. Young in their first year comprised 39 percent of all those marked, but were represented by only 18 percent among the recaptured 1946-1947 survivors.

Reproduction.—Data were collected for the stages of the reproductive cycle occurring in late March, April, May, and June, the only season when breeding females were found. The proportion of adult females, about half, that had no enlarged ova during the breeding season, indicated that in an individual female, breeding occurs only in alternate years. Of 33 adult females dissected in 1940 and 1946, sixteen had enlarging ova, and seventeen lacked them. Determination of litter size by egg counts during the breeding season is made difficult by the fact that the ova are only beginning to enlarge then. Some are much larger than others and the smallest ones are not destined to develop into young snakes during the current growing season. The larger ova tend to form a fairly well defined group, but some are intermediate in size. In the following table of egg counts, based on the combined data of six different years, length measurements apply to the largest egg in each female, and only those eggs more than half the length of the largest ones in each snake are included in the counts.

TABLE 12.—Number and size of eggs in adult female rattlesnakes.

Date	Head and body length of female (in mm.)	Number of eggs	Length of eggs (in mm.)	Date	Head and body length of female (in mm.)	Number of eggs	Length of eggs (in mm.)
Mar. 21	820	7	12	Apr.	—	14	—
Mar. 26	767	11	15	Apr.	—	7	—
Apr. 8	700	4	17	May 2	840	19	10
Apr. 9	847	15	6	May 3	680	5	14
Apr. 10	736	6	10	May 5	832	8	24
Apr. 11	763	5	12	May 8	793	11	22
Apr. 14	826	14	7	May 10	812	8	13
Apr. 14	682	16	5	May 10	853	10	22
Apr. 14	880	25	8	May 11	737	9	21
Apr. 14	830	7	9½	May 15	885	8	20
Apr. 16	870	9	15	May 23	835	11	—
Apr. 21	814	14	12	Jun. 3	754	7	18
Apr. 22	805	9	7	Jun. 11	820	5	30
Apr. 24	752	11	—	Jun. 13	873	9	33
Apr. 26	720	8	12	Jun. 13	770	11	26
Apr. 27	840	11	12	Jun. 16	855	9	33
Apr.	—	9	—	Jun. 19	788	7	30
Apr.	—	7	—				

Litters probably averaged somewhat smaller than the 9.9 average of eggs per female, as some may not be fertilized, and some prenatal mortality might be expected. In an earlier report (Fitch and Glading, 1947: 110) it was indicated that about 171 days elapse between the dates of spring mating and of fall appearance of newborn young. Only the latter part of this interval is the gestation period, since ovulation, and fertilization by the stored spermatozoa, does not occur until perhaps two months after copulation. At the time of copulation the ovarian eggs are usually about 10 to 12 mm. long, only a fraction of their size at maturity, and of whitish color. They make steady growth during subsequent weeks.

In the spring sample, approximately one-fourth were females large enough to be sexually mature. If this ratio is correct, and if individuals produce litters, of about ten young, in alternate years only, then the population is somewhat more than doubled (1.25 to 1) by the annual fall brood. The extent of juvenile mortality before, during, and just after the first hibernation may be judged by the fact that less than one-fourth of the spring sample is comprised by these small young. However, perhaps the young are more easily overlooked than other sizes, and are inadequately represented in the sample.

Movement.—Place of capture was recorded for each snake taken and most were returned to the same place for release. Successive captures of 156 individuals taken a total of 359 times indicated extent of movement; 126 were recaptured once, 20 were recaptured twice, 6 three times, 2 four times, 1 five times, and 1 six times. Of these recaptured snakes, 82 were taken after more

than six months, 39 others after one month or more, and the remaining 35 were taken after intervals of less than one month.

There was much variation in extent of movement. One snake moved a quarter of a mile overnight. In a number of other instances individuals were known to have moved at much slower rates, but with a tendency to wander progressively farther from the point of original capture over periods of weeks. During the early stages of the study it was believed that the snakes wandered at random (Horn and Fitch 1942: 121) because definite "territories," home ranges or home bases were not apparent.

Stickel and Cope (1947: 132) discussing the data on rattlesnakes in this earlier paper from the San Joaquin Range, have suggested that the long trips of a few individuals and the wanderings of juveniles influenced the conclusion that the snakes may wander indefinitely, and that the localism of many others suggested limited home ranges. The present writer, after accumulating more records over periods of years, independently arrived at the same conclusion.

For several individuals series of records were obtained over periods of days, showing that they moved circuitously and by slow stages, with the more extensive boulder piles and large squirrel burrow systems as focal points. A certain burrow system or rock pile might serve temporarily for shelter and prowling over a period of days or even weeks, but eventually would be left more or less permanently as the snake wandered away to an adjacent one and finally to more remote parts of its range. In view of the sluggish habits, many weeks might be required to make the circuit or crossing of its prowling range. There is no evidence of any one "home base" and probably any convenient shelter is used. The snakes were too secretive and records too few to demonstrate whether one covers its range regularly and over a definite route, or returns to the same hibernation den in fall.

Snakes recorded came from all parts of the 4600 acre Experimental Range but with concentrations of records in two relatively small areas. One of these was the vicinity of the Range headquarters where the activities of numerous persons greatly increased the likelihood of discovery of any snake present. Rattlesnakes found here were mostly killed by their discoverers, and the few obtained alive were released elsewhere, so that they would not constitute a hazard. The second area of concentrated records was about ¾ mile from the headquarters and was a rectangular 160 acre pasture where field work, primarily live trapping and observation of rodents, was carried on almost daily throughout the year by one or several persons. Almost half as many snakes were found on this area as on the remainder of the Range—an area some 28 times larger—due to the concentration of field work. Opportunity to capture those marked snakes that made unusually long movements therefore would have been poor.

Of the 156 marked snakes recaptured, two had moved more than a mile, 14 others more than half a mile, and 14 others more than a quarter of a mile. The great majority, 126, had traveled less than a quarter mile, and 52 of these had traveled less than 100 yards. Records of the 35 snakes recaptured after intervals of less than a month are judged to be unsuited to show extent of home

ranges, since they might not have had time to move across their entire prowling areas at the characteristically slow rate of travel. Most of this group, recaptured after short intervals, were small young.

The remaining 121 records summarized in Table 13 include 82 snakes recaptured after intervals longer than 6 months, and 39 recaptured after 1 to 6 month intervals. These two groups are combined because their trends are closely similar despite the differences in elapsed time. Also, because separate calculations showed no significant difference in average movement between young and adults within each sex, their data are combined in this table.

Stickel and Cope (1947) have emphasized that in any animal species (referring particularly to snakes) different types of movement may occur, some of which may not be confined to the usual home range. It seems evident that in the present study, several of the longer movements recorded were not confined to the limits of a home range, but represent shifts from an original area to another one, or some other type of wandering beyond the limits of a typical home range.

The great majority of records (85 percent) are under 1500 feet, and show fairly even dispersion up to this distance. But for greater distances, up to 1.6 miles, there are only scattered records, mostly of males. It seems probable that most or all of these records beyond 1500 feet represent shifts away from the original home range. Disregarding these 17 longest movements, the average distance for the remaining 67 males is 630 feet, and, for the remaining 37 females, 467 feet.

Obviously the full extent of the range cannot be shown with only one or a few recaptures of an individual. The distances between sites of such captures

TABLE 13.—Distances moved by 121 marked rattlesnakes in periods of one month to nine years.

Distances in feet	Number of males	Number of females	Percentage of total
0- 300	21	19	33
301- 600	13	7	16
601- 900	16	4	16
901-1200	9	5	12
1201-1500	8	2	8
1501-1800	1	—	1
1801-2100	2	—	2
2101-2400	—	—	—
2401-2700	1	0	1
2701-3000	5	1	5
more than 3000	4	3	6
Totals	80	41	100

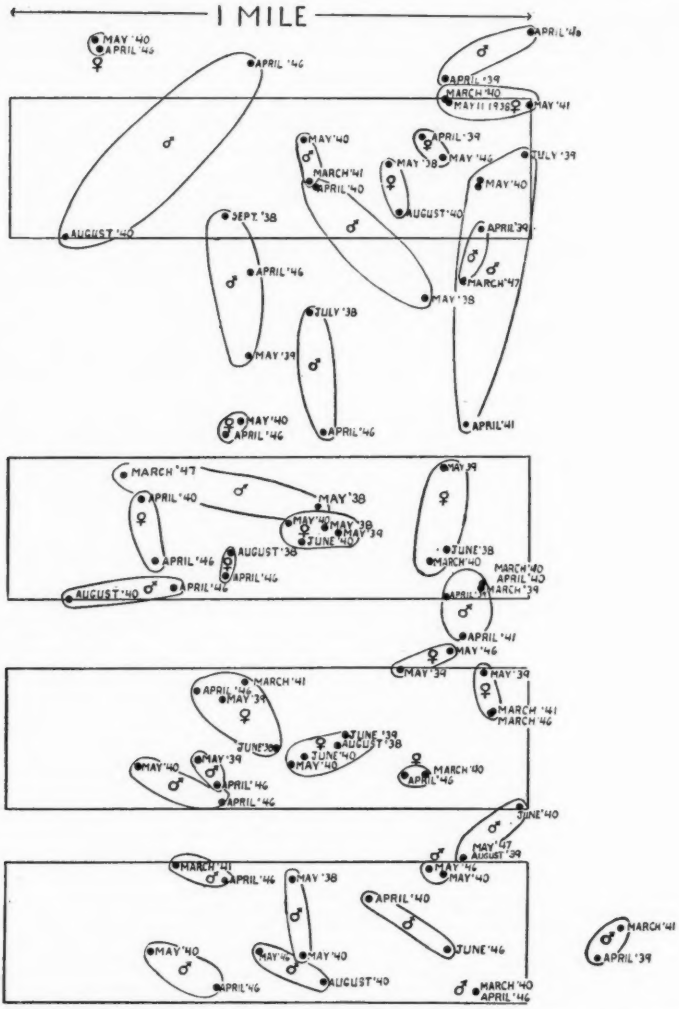

Fig. 7.—Movements of marked rattlesnakes in intervals between captures over periods of years. Each line encloses the records of a single snake, and all are shown in relation to the same mile long and quarter mile wide pasture where most field work was done. All those marked in this area and recaptured after two years or more are included. The trends were similar for many recaptured after shorter periods. Tendency to remain within familiar areas is apparent. Males, on the average, range more widely than do females.

would average only about half the diameter of the entire range, which might amount to nearly 30 acres in males, and approximately 16 acres in females, assuming it to be roughly circular in shape.

Stickel and Cope (op. cit.) found that the blacksnakes (*Coluber constrictor*) and pilot blacksnakes (*Elaphe obsoleta*) marked by them and recaptured after intervals up to two years usually made movements of a few hundred feet, comparable with those recorded for rattlesnakes in the present study.

Though young are apparently similar to adults in the extent of their usual prowling ranges, they may be more inclined to wander into new and distant areas. This was indicated by the unbalanced ratio of only 3 adults to 54 first year young (with one to four rattles) taken in the vicinity of headquarters, 1938-1940. When the present study was commenced in 1938, the rattlesnake population of this small area had been decimated, especially in 1935-1937, when many persons were engaged in construction of buildings and installation of equipment. For many years previously the site had been a ranch headquarters. As a result of all this human activity, numbers were kept at a level

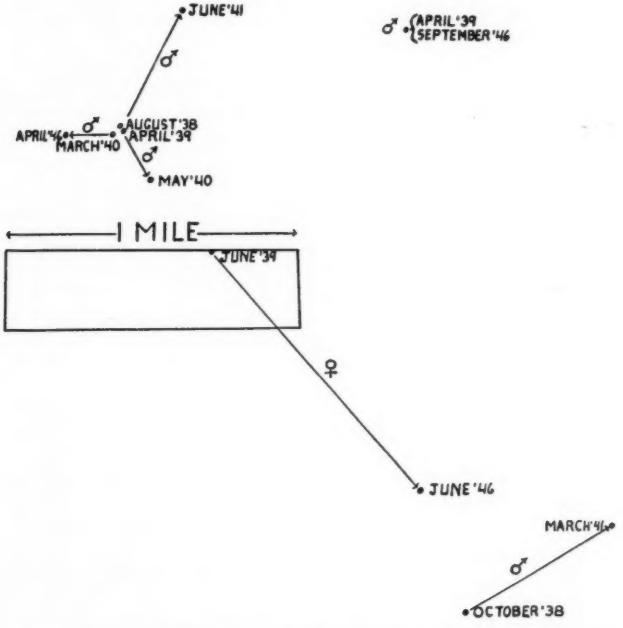

Fig. 8.—Movements of several marked rattlesnakes recaptured at distances from the mile-long study area.

far below that of the remainder of the Range, and the majority of those killed each year were recent arrivals.

Complete lack of any homing tendency was apparent in 14 marked snakes recaptured of a group of 59 released at distances from their sites of original capture. Many of them were originally captured in the headquarters area. If they had made homing movements, the chances of finding them there again would have been good. The records of the 14 recaptured are presented in Table 14.

The lack of wandering tendencies and disposition to remain in small areas in these individuals of the Pacific rattlesnake contrast with findings regarding the canebrake rattlesnake (*Crotalus horridus atricaudatus*) in Georgia. Neill (1948: 113) tentatively concluded that the population of canebrake rattlesnakes over an area of at least a 20 mile radius converged to a central denning area, following well-defined routes of travel in thick woods along streams. Evidence for this was provided by the frequent finding of snakes in late August at certain stream crossings. These snakes were always moving in the same direction, toward the denning area.

Numbers.—Population densities of snakes cannot be readily determined, as secretiveness, periods of inactivity, erratic nature of movements, and unknown rate of population turnover are obscuring factors. The best basis for calculating the population density of rattlesnakes was found in the ratio of those recaptured to others on the 80 acre area (1/2 by 1/4 mile) where intensive field work was done each month for a continuous four-year period. This area was fairly representative of the Range as a whole, but was somewhat more open with comparatively few rock outcrops and brush patches. Since extent of activity changes a great deal during the course of the season, comparable samples could be obtained only by considering each year as a separate sampling

TABLE 14.—Distance traveled by marked snakes transferred to new areas.

Head-and-body-length in mm.	Sex	Months elapsed	Distance (in feet) traveled from point of release
1091	♂	72—	750
1035	♂	2—	1600
1000	♂	2—	360
805	♂	12	800
750	♂	7+	750
720	♂	24+	300
1011	♂	3+	1000
561	♂	21+	1000
500	♂	6	950
394	♂	1+	400
383	♂	11+	500
359	♂	1—	300
330	♂	[5 days]	no movement
321	♀	11—	1050

period. Extent of home range must be considered in computing the population density from the number actually present on an area. Home ranges are larger for males than for females, so it is necessary to deal with the data for the sexes separately in attempting to determine numbers present.

A hypothetical total population is derived from an equation wherein the number of snakes present is calculated by the total number caught on the area one year, and the ratio of these marked ones among the total caught during the following year.

$$\frac{\text{Population in 1938}}{\text{Number recorded in 1938}} = \frac{\text{Number recorded in 1939}}{\text{Number recorded in 1938 and recaptured in 1939}}$$

In this computation, the "number recorded in 1939" does not include young of the year. As they were born after the 1938 sampling, their inclusion would distort the ratio.

Records of recapture of rattlesnakes in separate years subsequent to their original marking totalled 109, for 84 individuals. However, the majority of these were either recorded outside the sample area, or were recaptured only after intervals of two or more years, hence could not be used for the census. The figures for the 80 acre area were as follows:

TABLE 15.—Number of rattlesnakes captured on an 80 acre area.

Year	Males			Females		
	Total captures	Recaptures from preceding year	Captures exclusive of young of the year	Total captures	Recaptures from preceding year	Captures exclusive of young of the year
1938	23	none	9	20	none	7
1939	46	3	13	36	1	13
1940	54	6	18	48	7	17
1941	11	4	7	6	2	4

These figures served for three separate censuses of each sex. For example:

$$\frac{x \text{ (number of males in 1938)}}{23 \text{ (number recorded in 1938)}} = \frac{13 \text{ (number recorded in 1939)}}{3 \text{ (number recorded in 1938 and recaptured in 1939)}}$$

$$3x = 299; \quad x = 99.6$$

Similarly, there were computed to be 138 males in 1939, and 94.5 in 1940. For the females numbers computed were: 260 in 1938, 85 in 1939, and 96 in 1940. Actually the numbers probably changed but little from year to year, and the differences in figures obtained reflect the margin of error to be expected with the amount of data available. In particular, the figure of 260 females for 1938 is evidently out of line, being based on a single record of recapture.

That population turnover in these snakes is slow is shown by the longevity of individuals. Therefore, it seems evident that variation in the results of the several census computations of different years arose mainly from inadequately small samples, rather than from changes in the number of snakes. To obtain a more adequate sample the three sets of figures, for successive annual samples were combined in each sex, as shown below:

Year	*Males*	*Females*
1938 (from 1939)	$\frac{x}{23}=\frac{13}{3}$	$\frac{x}{20}=\frac{13}{1}$
1939 (from 1940)	$\frac{x}{46}=\frac{18}{6}$	$\frac{x}{36}=\frac{17}{7}$
1940 (from 1941)	$\frac{x}{54}=\frac{7}{4}$	$\frac{x}{48}=\frac{4}{2}$
Combined	$\frac{3x}{123}=\frac{38}{13}$ $x=120$	$\frac{3x}{104}=\frac{34}{10}$ $x=118$

These figures probably provide a fair idea of the average spring and summer population ranging over the 80 acres.

It is evident that many of the rattlesnakes censused on the 80 acres also ranged extensively outside of it (Figure 7). Assuming that the males censused ranged collectively over not only the 80 acres but a peripheral area 630 feet wide (i.e. half the diameter of a home range, see Dice, 1938: 119-130) then their collective range would amount to 80 + 143.5 or 223.5 acres. Their population density would be .538 snake per acre. The 118.0 estimated females on the area would likewise range collectively over a peripheral strip 467 feet wide, amounting to 100.88 acres, and their total collective range would be 180.88 acres. The female population density would thus be .654 per acre, which added to the male figure would indicate a rattlesnake population density of approximately 1.19 per acre. It is not meant to imply that this constitutes a precise measurement. With the small samples obtained, the long time between sampling periods, and the existence of unmeasurable variables, a wide margin of error, perhaps 30 percent or more, seems probable. The male-female ratio of 1 to 1.21 indicated by these figures is surprising in view of the

numerical superiority of males in all samples. The true sex ratio is obscure, but females may be somewhat more numerous than males. Their more secretive habits would cause them to be found in smaller numbers.

Obviously the census is affected by the rate of population turnover between samplings, and in a year interval, replacement of some snakes eliminated by death or emigration would occur. For the adults at least, neither factor would seem to be of major importance, but in the immature snakes death and wandering might result in a substantial population turnover. The extent to which these factors operate to distort the year-interval census may be judged from the results obtained with censuses of two to seven year intervals on the same area. As a basis for this, recaptures of marked snakes were recorded as follows: 1940 from 1938, 4 females; 1941 from 1939, 1 male and 1 female; 1941 from 1938, 1 female; 1946 from 1938, 1 female; 1946 from 1939, 3 females; 1946 from 1940, 2 males and 1 female; 1946 from 1941, 1 female. These combined samples, representing an average 4½ year interval, yielded a figure of 372 snakes on the 80 acres, as against 238 snakes computed with the one year census interval.

Feeding.—A total of 285 prey items of 19 kinds were recorded for rattlesnakes on the Range. In a previous report (Fitch and Twining, 1946) 177 of these records were included. In 184 instances food items were identified from snake stomachs, or were found with snakes in the field before swallowing commenced; 92 items were identified from snake scats, and 9 from residual hairs of prey animals in cloacae of snakes having empty stomachs.

Palping of live snakes provided the most satisfactory method of investigating the food habits in connection with the population studies, however, only a small proportion of the snakes examined had food that could be palped. Snakes that have recently fed probably tend to remain inactive in inaccessible places, where they are much less apt to be found, than are those that are hungry and actively prowling.

By the combined methods used the following list of prey animals was compiled: 116 ground squirrels, 32 kangaroo rats, 29 cottontails, 21 pocket mice, 13 pocket gophers, 12 fence lizards, 9 spadefoot toads, 8 woodrats, 8 brush mice, 7 white-footed mice, 7 meadow mice, 6 brown-shouldered lizards, 5 whiptail lizards, 3 skinks, 2 rock mice, 2 quail, 2 towhees, 1 chipmunk, and 2 unidentified rodents. The various prey species differed greatly in availability or acceptability to the snakes. The mere listing of numbers of occurrences for each kind does not adequately express either the relative importance as part of the rattlesnakes' diet, or the importance of rattlesnake predation in its ecology. The several kinds of prey differ greatly in size.

In many instances it was possible to weigh the animal that had been eaten, after palping it from the snake's stomach. Such data for the various kinds represented provided a basis for calculating their relative weight. Most often, the prey animals killed by the snakes were immature ones, which were more easily caught than adults and more abundant during the "snake season."

However, this factor differed according to the kind of animal, since, for instance, only small cottontails could be swallowed, whereas various kinds of mice and lizards were often taken as adults.

A series of 18 ground squirrels from snake stomachs weighed from 121 to 460 grams, with an average of 206. All were young, mostly 1/3 to ½ the usual adult weight, and it appears likely that adult ground squirrels are not often eaten. When instances do occur, the squirrels must be individuals below average size, caught by exceptionally large rattlesnakes. The only weight recorded of a cottontail from a rattlesnake stomach was likewise 206 grams. All other cottontails recorded were also young that probably approximated this figure. For other kinds of prey the average weights were: kangaroo rat (1), 60 grams; pocket mouse (3), 12 grams; pocket gopher (3), 67 grams; fence lizard (3), 15 grams; woodrat (1), 71 grams; brush and rock mice and white-footed mouse (4), 15 grams; brown-shouldered lizard (2), 4.3 grams; whiptail lizard (2), 12 grams; quail (1), 66 grams; towhee (1), 50 grams; spadefoot toad (1), 8.5 grams. No weights of the chipmunks, meadow mice, or skinks actually eaten were obtained, but for these species weights of 100 grams, 30 grams, and 20 grams respectively are thought to be representative. Assuming that for each species those occurrences unweighed from scats or stomachs, averaged about the same as the weighed samples, the approximate composition by weight of the rattlesnake's food can be shown. The recorded food was estimated as about 34.7 kilograms or 77 pounds.

From this list it will be seen that the ground squirrel is by far the most

TABLE 16.—Composition, by weight, of rattlesnake food.

Kind of prey	Average weight in grams	Number of occurrences	Percentage, by weight, of total prey items
Ground squirrel	206	116	68.8
Cottontail	206	29	17.3
Kangaroo rat	60	32	5.5
Pocket gopher	67	13	2.5
Woodrat	71	8	1.7
Mice (*Peromyscus boylii, truei, maniculatus*)	16	17	.8
Pocket mice (*Perognathus inornatus, californicus*)	12	21	.7
Meadow mouse	30	7	.6
Fence lizard	15	12	.5
Quail	66	2	.4
Towhee	50	2	.3
Chipmunk	100	1	.3
Spadefoot toad	8.5	9	.2
Whiptail lizard	12	5	.1
Skink	20	3	.1
Unidentified rodent	(20)?	2	.1
Brown-shouldered lizard	4	6	.1

important prey species, and makes up nearly 69 percent of the food. The cottontail, kangaroo rat, gopher, and woodrat appear to be of secondary importance and are the only other kinds that separately amount to as much as one percent. The various mice, lizards, and birds that are also eaten amount to hardly more than traces.

A group of small prey species including "mice" of the genera *Peromyscus* and *Perognathus*, whiptail, brown-shouldered and fence lizards, and the spadefoot toad, which combined made up only about 2½ percent of the total food weight, comprised nearly all the food of the small young, and comprised just under one-fourth of the total recorded items. These smallest kinds of prey were not found in the adult rattlesnakes. Kangaroo rats and gophers offered to three adult and two small young rattlesnakes in confinement together were eaten by the adults, but twice when pocket mice were offered, they were apparently ignored by the adults, and were eaten by the juveniles. Young rattlesnakes are not known to feed upon invertebrates, but depend upon small rodents, lizards and toads, and must feed frequently.

The scats collected could not be closely dated as to time of deposition, since they probably remain intact and little changed in appearance over periods of months in the dry season. However, the items found in stomachs must have been eaten within a few days of the time they were recorded. The seasonal distribution of these records closely paralleled the changing numbers of snakes collected from month to month.

Including 203 recaptures of marked rattlesnakes, a total of 1128 captures were recorded (exclusive of those in 1947) and all were tested for food items. In 164 snakes, about 14.5 percent, food was found. Other snakes may have contained partly digested food in the intestines, or they may have had food in their stomachs too far disintegrated to be palped. Only six snakes contained more than a single item. Two of these each had eaten two ground squirrels, one had eaten two meadow mice, one had eaten four young cottontails and another had eaten three (of a litter in each instance). One had eaten a pocket mouse and a fence lizard.

About 84 percent of the stomach food items were recorded in April, May, and June, with nearly 70 percent in April and May. These spring records may not be entirely representative of the year-round feeding. Snakes obtained after the end of June were mostly small ones, with a high proportion of mouse and lizard in their food. The ground squirrels eaten in four different years were recorded in April (32), May (28), June (8), July (3), and August (1, as residue of hair in cloaca, probably eaten in July). Cottontails occurred in April (8), May (14), and June (3). Late litters of cottontails are still in the nests in May and possibly in early June, but soon after leaving the nest these young have grown too large to be swallowed, even by large rattlesnakes. Young ground squirrels usually appear above ground in April (subject to several weeks variation in response to weather conditions). They are then small enough to be swallowed easily by adult or even half-grown rattlesnakes, and their emergence corresponds with the season of maximum rattlesnake activ-

ity. But in late summer the young squirrels are hardly distinguishable from adults and are probably too bulky to be eaten by any but exceptionally large rattlesnakes.

Notwithstanding the seeming unavailability of their favorite spring prey in summer, adult rattlesnakes doubtless continue to feed at intervals during the dry season. The two adult females and a subadult male kept through the dry season in confinement, with natural conditions simulated in most respects, never showed themselves in the daytime during summer, but were often active after dark. They fed at intervals of a few weeks and lost weight rapidly between these meals, indicating that a food weight of at least twice the snake's body weight is necessary to maintain it in good condition throughout the growing season. This would mean consumption of at least five well distributed meals of ordinary size. In an adult snake's annual feeding, probably not more than two or three of these meals, taken in spring and early summer, would be ground squirrels.

The kangaroo rat is about the optimum size for an adult rattlesnake's meal. In the latter part of the dry season it may bear the brunt of predation pressure. Evidence of this is afforded by the scatological material, gathered at different dates throughout the late spring and summer. Though the scats cannot be accurately dated as to time of deposition, some were doubtlessly voided by snakes during nocturnal prowling in hot weather of the season when hardly any stomach items were obtained from adult rattlesnakes. The outstanding differences between the trends of stomach items and scat items obtained the same year are that in the scats there is a lower percentage of cottontail occurrences (16.1% compared with 33.3%), a higher percentage of kangaroo rat (26.7% as compared with 5.8%), and of ground squirrel (41.1% as compared with 26.4%).

The gopher was represented by an even smaller percentage (2.2%) in scats than in stomachs (9.2%) suggesting that like the squirrel and rabbit, it becomes less available in the dry season. The shift from surface to underground feeding, diminution of digging activity, and cessation of breeding in the dry season, are all factors that tend to make the gopher less accessible in the safety of its burrow systems. The holes are usually plugged against the entrance of snakes or other slender-bodied predators.

Evidence that rattlesnakes strike and kill many animals that they do not eat was set forth in a previous paper (Fitch and Twining, 1946). On June 10, 1938, a rattlesnake was seen prowling in the vicinity of a burrow system where there were two young squirrels, about twenty feet apart, apparently dying from snake bites. On May 12, 1938, an informant told of seeing a young squirrel lying in the road, apparently dying from snake bite, and when the spot was visited, another squirrel was seen running erratically, as if injured. A third, running through rocks and brush, was struck by a waiting rattlesnake, and died almost immediately. Another time two young squirrels frightened into the same hole popped out and back in again several times within a few seconds, and gave shrill squeals while underground. Then a rattlesnake, too small to have eaten them, emerged, rattling, and attempting

to escape. On April 25, 1947 a young squirrel was heard to give a shrill squeal of distress, and a few minutes later was found lying dead beside its burrow. A short time later a rattlesnake was found to have eaten this squirrel and a second young squirrel lay dying ten feet away. These specific instances suggest that often rattlesnakes prowling where there are litters of young squirrels may strike several in succession, although ordinarily only one will be eaten.

On May 2, 1940, as several young squirrels alarmed by the investigator escaped into their burrows, one was struck by a rattlesnake coiled in a depression within the burrow entrance. On April 24, 1940, a young squirrel running to its burrow in a rock outcrop was struck by a rattlesnake lying concealed in a vertical crevice overlooking the burrow entrance. On June 18, 1940, a squirrel was heard to give a sharp distress squeal and was located on a sloping boulder. Its body was tense, and it tended to reel over backward or sidewise as it escaped into a crevice. Evidently it had just been bitten. In eight other instances ground squirrels were found dead, and when dissected, showed evidence of rattlesnake bite. In six instances kangaroo rats found dead on the ground surface were identified as rattlesnake victims by fang punctures and internal hemorrhage. In one instance the rattlesnake was seen to trail and find the rat, and drag it several yards to the shade of a bush before swallowing it. In several instances the animal killed had already begun to decompose when found, and obviously it would not have been eaten subsequently by the snake that struck it.

Natural enemies.—Many instances of predation on rattlesnakes by their natural enemies were obtained through the finding of their remains in scats or pellets, or through actual field observations. An idea of the frequency with which various predators take rattlesnakes may be gained from the following tabulation:

TABLE 17.—Instances of predation on rattlesnakes.

Kind of predator	Total vertebrate prey items recorded	Number of rattlesnake occurrences in food items
Red-tailed hawk	4110	74
Coyote	1924	17
Horned owl	968	4
Roadrunner	not studied	3
Cooper's hawk	42	1

The red-tailed hawk and coyote appear to be the most important destroyers of rattlesnakes; for the hawk they were computed to comprise around two percent, by weight, of the diet; for the coyote around .8 percent. The roadrunner, however, might be found to take more young rattlesnakes than all the other predators combined if its numbers and feeding habits were better known. Each of the three records of roadrunner predation were obtained through chance observations of these birds carrying rattlesnakes. One seen at close

range had a two-foot rattlesnake dangling from its bill, still writhing though its neck was broken about two inches behind the head.

Other local predators, not adequately investigated, but which might be suspected of predation on rattlesnakes, especially small ones, include the gray fox, badger, striped skunk, king snake, California racer and sparrow hawk. On one occasion a California jay was seen warily circling a small rattlesnake coiled on a lawn; it probably could have overpowered this snake if it had attacked.

Most of the predators that kill rattlesnakes usually take only small ones and probably would not risk attacking an adult under ordinary circumstances. That its venomous qualities, or perhaps its strident warning are heeded by predators, is evidenced by the few found in pellets and scats as compared with the more frequent occurrences of the scarcer gopher snake. Red-tailed hawks had taken 204 gopher snakes to 74 rattlesnakes; coyotes, 79 gopher snakes to 17 rattlesnakes; and horned owls, five gopher snakes to two rattlesnakes.

On the 4600 acres of the Range human beings are probably more destructive in their effect on the rattlesnake population than are any other predators. This is not so much because of the actual numbers killed as because of the high proportion in this group of old adults, which make up the breeding stock and are relatively safe from natural enemies. Numbers recorded as killed during five different years are as follows: 1935—326; 1936—185; 1937—145; 1938—58; 1939—105. Probably many others were killed that were not recorded, especially in 1938, as interest in the study and extent of cooperation were variable. On more remote parts of the area the killing has probably had little effect on the population, whereas, in the vicinity of headquarters the numbers are held at a low level by the killing of those that move in from adjacent pastures.

Besides those snakes that are killed by natural enemies or man, and those probably dying from lack of food, some are eliminated by accidental deaths. A small one was found crushed where it had been stepped on by a cow. A large adult male found dead, and dissected, had fang punctures and typical internal hemorrhage as seen in other animals that have died from rattlesnake bite. A pair of live rattlesnakes were found nearby. The cause of death was not evident in a half-grown snake found in a typical resting coil. One of the young rattlesnakes kept confined in the outdoor pit finally killed and ate a pocket mouse one night after having become somewhat emaciated. The following morning its movements were so handicapped by its relatively large meal that it was unable to reach the usual shelter in time and was killed after short exposure to sunshine. Such accidents as this might occur under natural conditions.

GOPHER SNAKE

The gopher snake on the area of the Experimental Range is less abundant than the rattlesnake. The recorded totals of 256 gopher snakes and 932 rattlesnakes, a ratio of one to 3.7, are perhaps a rough index to the relative

population densities of the two species, since they are somewhat similar in habits and habitat preferences. However, the gopher snake is more likely to choose situations having a thick cover of vegetation, while the rattlesnake prefers barren and rocky places. The relative abundance of the two kinds on different parts of the Range therefore varied. On the ungrazed headquarters area, with an accumulation of rank vegetation, the gopher snakes taken outnumbered rattlesnakes one to .9. This was partly because rattlesnakes were kept killed off by human beings. On more typical range land, the 160 acres where rodent studies were carried on, 63 gopher snakes and 273 rattlesnakes were recorded, a ratio of about one to 4.3.

General Behavior.—In rhythms of seasonal and daily activity, the gopher snake parallels the rattlesnake in this locality. It emerges from hibernation at about the same time in March or April, depending upon the weather, and is diurnal until hot weather sets in. Then it tends to becomes crepuscular and nocturnal during most of the dry season. It is more active than the rattlesnake, and is often on the move when seen in the open. Of the 256 recorded, 12.9 percent were with their prey, or had food in their stomachs, but many of these had eaten more than a single item—usually from the same litter of young rodents, or clutch of eggs. The food is secured in most instances by active prowling, often consisting of a search for, and raiding of, nests of small mammals or birds to obtain the helpless young, or eggs. The snakes are activated by sight or scent of any small animal moving near them, and may stealthily approach to seize and constrict it. In eleven instances in which prey weight and snake weight were available, the prey weight ranged from 4.4 to 64.0 percent of the snake weight and averaged 34.8 percent, approximately the same ratio as obtains for the rattlesnake and its prey.

Growth.—Newly hatched gopher snakes taken in late September (3), October (24) and November (1) averaged around 400 mm. in length; 23 were between 350 and 450, while five were less than 350 mm. Subsequent growth may be inferred by the sizes of those found in spring months.

TABLE 18.—Seasonal occurrence of young gopher snakes in different size groups (head-and-body-lengths in mm.).

	301-350	351-400	401-450	451-500	501-550	551-600
Sept., Oct., Nov.	5	11	12	0	0	0
March	0	4	4	1	0	0
April	0	10	4	4	3	0
May	0	2	6	9	10	2
June	0	0	2	1	1	1
July	0	0	0	1	1	0

Most of the young have grown more than 100 mm. during late spring following their first hibernation. Comparatively few half-grown snakes were taken, and they could not be sorted into age groups.

Several marked gopher snakes that had made substantial growth were recaptured, but these are too few to permit reconstruction of the normal growth pattern.

TABLE 19.—Growth of recaptured young gopher snakes.

Number of months elapsed between captures	Sex	Head-and-body-length in mm.	Weight in grams
3—	♀	375 to 390	14 to 16
5—	♂	438 to 716	27 to 83
5+ (5 in hibernation)	♂	323 to 330	9 to 20½ (with food)
7— (5 in hibernation)	♀	379 to 420	19 to 24
12 (5 in hibernation)	♂	515 to 868	37 to 242
20+ (10 in 2 hibernations)	♀	692 to 1002	88 to 329

Growth rates much more rapid than the average for rattlesnakes are demonstrated, and if their trend is representative, a two year old gopher snake would have a head and body length of more than 800 mm. Beyond this length, growth probably slows down. A male marked in May 1939, when it had a head and body length of 874 mm., was identified from a cast skin found near the same place 36 months later. Measurement of this skin indicated a length increase of about 270 mm. in this three year interval; but the skin had probably stretched, so that the actual growth was somewhat less.

Imler (1945: 267) concluded from his study of the subspecies *sayi* in Nebraska, that young grow about 15 inches the first year and seven or eight inches the second year. The California gopher snake may follow this trend, but some of those marked and recaptured had made more rapid growth. Several other subadult and adult snakes (all males) made notable gains in the intervals between captures.

TABLE 20.—Growth in medium to large recaptured gopher snakes.

Number of months elapsed between captures	Head-and-body-length in mm.	Weight in grams
11—	1100 to 1143	? to 515
11+	1181 to 1224	509 to 584
71—	1270 to 1550	589 to 1148
73—	1273 to 1350	470 to 840

These records show that adults may continue to increase in size slowly over periods of years, after the relatively rapid growth bringing them to minimum adult size. For 267 gopher snakes measured, size groups were as follows: 96—300 to 600 mm.; 19—601 to 900 mm.; 57—901 to 1200 mm.; 56—1201 to 1500 mm.; 28—1501 to 1800 mm.; 1—over 1800 mm.

For the 243 gopher snakes that were sexed, a ratio of 1.38 males to one female was obtained. For 86 young under 600 mm. in length, the ratio was 1.15 males to one female. Except for newly hatched young taken in the fall, most of the gopher snakes were collected in the spring months, late March, April, May and June. A total of 203 were taken in these months. As old and

TABLE 21.—Size groups in a spring sample of the gopher snake population.

Head-and-body-length in mm.	Number of snakes and percentage of total
300 to 600 (Yg. mostly less than 1 yr. old ?)	66 (32.5%)
601 to 900 (Yg. 1 to 2 yrs. old ?)	13 (6.4%)
901 to 1200 (Small adults)	51 (25.1%)
1201 to 1500 (Adults)	52 (25.6%)
1501 to 1800 (Large adults)	21 (10.4%)

young of both sexes are active at this time of year, the composition of the population may best be sampled then.

Nearly one-third of the spring population consists of the small young, only a few months old. As a group these young must have already been much reduced by natural mortality, for in the fall at the time of hatching, they are much more numerous.

No figures are available as to the number of eggs produced by female gopher snakes in this locality. Imler (1945: 273) records an average of 12.8 eggs per female in *sayi* of Nebraska. Klauber (1947: 58) records an average of only 6.8 (3 to 12) eggs for thirteen clutches of the southern California subspecies *annectens*, laid in captivity. He records nine other egg counts from the subspecies *annectens*, *affinis*, *deserticola*, and *catenifer*, for which the average number is 10.2. Schmidt and Davis (1941) record four clutches of 10 to 18 eggs, average 14, in *sayi*, and clutches of 10 and 19 in *catenifer*.

Mortality rate is highest in the young during their first few weeks of life, between the time of hatching and retirement into hibernation. Elimination of more than 80 percent of the young that emerge from their first hibernation, during the subsequent year, is indicated by the relatively small number surviving in the 600 to 900 mm. group. Many kinds of predators including hawks, owls, coyotes, foxes, and king snakes, frequently prey on gopher snakes and take mainly the young ones. Those that have attained a length of 900 mm., small adult size, are probably relatively safe. The adult population must con-

sist of the accumulation of many years' crops of young. That these snakes are long-lived was indicated by the recapture after approximately six year intervals of two that were marked when already large adults.

Movement.—In 28 instances in which site of release and of recapture were recorded for marked gopher snakes, extent of movement was measured. In one doubtful record, an adult male apparently moved 6720 feet, in 69 days, but there may have been an error in recording its place of release. Another adult male moved 2590 feet in 23– months, another 1550 feet in 22– months, and a medium sized one moved 1840 feet in just less than a year. The remaining 25 records, seven of them pertaining to intervals of more than a year, were all of less than 1000 feet.

TABLE 22.—Distances travelled by marked gopher snakes.

Distance of movement in feet	Number of snakes	Average intervals between captures (months)
0 to 300	9	9.8
301 to 600	10	19.1
601 to 1000	5	4.8

Females comprised 14.3 percent of those moving more than the median 460 feet, and 42.9 percent of those moving less than this median distance. The longest female movement recorded was 720 feet, perhaps indicating that females are more localized or sedentary than are males. The six records of recaptured young showed about the same trend as the larger number of records for adults, and it is not evident that the young are either more or less localized. The long-time records are of course most significant in indicating extent of movement. Two adult males, after approximately six years were recaptured at distances of 500 and 450 feet respectively and another was 200 feet away after three years. Evidently individuals are more or less permanently attached to limited areas of a few hundred feet diameter.

Feeding.—A total of 72 food items were recorded from stomachs of gopher snakes representing 12 or 13 prey species, as follows: 25 mice (*Peromyscus*, mostly small young, in litters of 6, 5, 4, 4, and 3, including the species *P. maniculatus, P. boylii,* and probably *P. truei*), 20 quail eggs (including parts of clutches from four different nests), 7 meadow mice, 5 ground squirrels, 3 woodrats, 3 cottontails, 2 each of pocket gopher, fence lizard, brown-shouldered lizard, one each of kangaroo rat, pocket mouse, and a small unidentified rodent. Many of these prey items were weighed, and assuming average weights for the others, the percentage by weight of the recorded food was computed.

A sample of this size cannot be expected to represent the food composition

accurately, but in this instance it is particularly distorted by the fact that one item, an adult cottontail eaten by a giant gopher snake, weighed about one-fourth as much as all the other 71 items combined. As a result the weight percentage of cottontail, 37.2 percent, is unrepresentatively high in the sample. By excluding this one extraordinary item, the following weight percentages are obtained, as shown in Table 23.

TABLE 23.—Composition of food of gopher snakes.
(Based on 71 records)

Kind of prey	Computed percentage of food weight	Kind of prey	Computed percentage of food weight
Ground squirrel	44.3	Meadow mouse	3.4
Woodrat	29.5	Fence lizard	1.5
Cottontail	19.7	Kangaroo rat	1.3
Quail egg	8.4	Pocket mouse	.6
Pocket gopher	6.4	Brown-shouldered lizard	.4
Mouse (*Peromyscus* sp.)	4.4		

It is noteworthy that 50 (69.5% of the 72 total) food items were young of rodents or eggs, which must have been found in the nest by the prowling snake, and of the 33 snakes with food, 13 (39.4%) were nest robbers. This contrasts with the findings concerning rattlesnakes in which only two, of a group of 164 containing food, had eaten animals (rabbits) too young to have left their nests.

On March 22, 1939, a young gopher snake seen to roll in a compact spherical mass from a rock pile to the ground, was found to be constricting a brown-shouldered lizard. Within a few minutes it swallowed the lizard despite some disturbance by the observer.

Seasonal distribution of feeding records for gopher snakes were: three in March; eight in April; fourteen in May; six in June; one in July; three in October. Of the seven dry season (June and July) feeding records, two involved adult males, and three adult females. Change to crepuscular activity during the hot months probably accounts for the paucity of records, but the adults as a group, including breeding females, do not disappear in this species as they do in the rattlesnake.

Natural enemies.—Investigation of the food habits of the large predators yielded more records of predation on gopher snakes than on any other reptile on the Range, even the abundant lizard species. Abundance, large size, active habits, and lack of speed render it liable to be found and eaten by those predators large enough to deal with it. The coyote is an important predator on this area. From 1924 vertebrate prey items in coyote scats collected on the Range in 1939 and 1940, there were 79 occurrences of gopher snake, which ranked sixth in frequency among the 35 kinds of prey represented. Assum-

ing each vertebrate occurrence to represent an adult prey animal of average weight for its species, the 79 gopher snake occurrences would have comprised six percent of the weight of coyote prey, exceeded only by rabbit with 45.4 percent and ground squirrel with 31.2 percent. However, it is probable that most of the gopher snakes eaten were young ones.

Gray foxes are perhaps as abundant as coyotes on the area, but no definite figures as to their numbers are available. A small sample of gray fox scats were collected in the following months: 2 in March; 7 in April; 6 in May; 1 in July; 1 in August; 3 in October; 27 in November; 40 in December. There were 102 vertebrate prey items, of which two were gopher snakes.

Red-tailed hawks are abundant on the area of the Range, a resident pair to half a square mile, and they prey frequently on reptiles, including the gopher snake, which comprised 14 of 625 prey items found at nests, and 190 of 3495 vertebrate prey items in a year round collection of pellets. In both nests and pellets gopher snake was fourth in frequency in a long list of prey species, exceeded in numbers only by the ground squirrel, cottontail, and pocket

Fig. 9.—Ground squirrel on its burrow mound, aggressively scolding a young gopher snake.

gopher. It was estimated to comprise 9.0 percent of the weight of prey items represented in pellets, and 3.8 percent of those items found in nests.

The catching and killing of a gopher snake by a hawk was observed on December 4, 1940, 8:12 a.m., by Freeman Swenson. The hawk, first seen perched on a high horizontal limb, "dropped off with wings half folded in a straight 250-foot glide to the ground. The prey was in the open on a flat rock but was knocked for a distance of several feet as the hawk struck it. Although partly hidden from view, the hawk could be seen flapping violently as it struggled with the prey on the ground. Investigation revealed that it had caught a five-foot gopher snake. The snake evidently had been seized first at the middle of the body, then caught by the neck, and bitten in the neck and head until dead. In eating the snake the hawk began on the head. About two minutes after the attack, the bird was flushed from the ground by the observer, and temporarily abandoned its prey, which was still writhing feebly, although its head was partly eaten. The ease and rapidity with which this large reptile was dispatched may have been due in part to the cool weather, preventing it from becoming fully active." (Fitch, Swenson and Tillotson, 1946: 233).

The Pacific horned owl is the most abundant large raptor of the Range, with a breeding population of at least one to 100 acres (Fitch, 1947). Among 968 vertebrate, pellet prey items of the horned owl, there were 20 occurrences of gopher snake, which ranged ninth in frequency among the many mammal, bird, reptile, amphibian and arthropod species. At 5:30 a.m. one summer morning, a horned owl flushed from beneath a live oak carried dangling in its talons a three-foot gopher snake, which caught on a barbed wire fence. The snake was still moving feebly but a piece of flesh was eaten from one side. One gopher snake was found among 517 barn owl prey items identified from pellets.

The ground squirrel may destroy more young gopher snakes than are taken by any kind of predator. The snakes often take refuge in rodent burrows, including those of the ground squirrel. On many occasions recently killed young gopher snakes badly mangled and lacerated have been found on the squirrel burrow mounds, where evidently they had been dropped by squirrels after having been fatally bitten in underground encounters. Squirrels finding small snakes in the open have been seen to approach menacingly as if about to attack, while scolding them (Fig. 9). To test this reaction further, a small gopher snake was placed in a cage with a tame female ground squirrel. "The squirrel, with hair fluffed out, moved around it with slow, tense steps. As the snake started to crawl away, she closed in and bit it sharply on the tail, but bounded back as the snake drew up on the defensive. When the snake started away again, she closed in for another quick bite, which was delivered on the posterior part of the body, seriously injuring the snake, and causing it to coil, writhing and thrashing. The squirrel grew bolder and moved up watching for an opening, then seized the snake in her forepaws, severed its spinal cord with a quick bite through the back, and again dropped it. This was repeated time after time, and each successive bite was placed farther up on the snake's body toward its head, until it was immobilized and helpless.

Then the squirrel picked it up in her forepaws and bit it through the head and neck. When finally left by the squirrel, its injuries resembled those of snakes found dead on burrow mounds, which almost certainly had been killed in similar encounters." (Fitch MS).

The snakes found killed in this way were all small young, with the exception of one about two feet long. Despite the meat-eating propensities of the ground squirrel, none of the snakes found killed on the burrow mounds had been eaten. Attacks are probably motivated by the instinctive antipathy of the squirrels for snakes of any kind.

On one occasion a clutch of gopher snake eggs was found, broken open with contents removed, and strewn over the vicinity of a squirrel burrow mound. The destroyer may have been a squirrel, and the eggs probably had been deposited in some part of the burrow system.

King snakes are known to prey on gopher snakes where the two species occur together. Only a single instance was recorded in the present study. The gopher snake involved was nearly as long as the king snake that ate it (Fig. 11). In view of the low king snake population, the small numbers of gopher snakes taken by them must be insignificant in comparison with those taken by the larger bird and mammal predators.

The badger, bobcat, striped skunk, roadrunner, Cooper's hawk and sparrow hawk are all locally common predators that might also be suspected of predation on the gopher snake, but nothing was learned concerning their numbers or feeding habits.

KING SNAKE

This species is much scarcer than either the rattlesnake or gopher snake. During the five years that field work was carried on, only 43 were recorded, as compared with 256 gopher snakes and 932 rattlesnakes. Actually the ratio of king snakes to these two species over the Range was probably lower than these figures indicate, since their population was concentrated in the headquarters area, where 26 of the 43 were found. There the extensive swale area, with persistent moisture in the dry season, and accumulation of rank vegetation favored their presence. Over most of the Range conditions were unfavorably dry and barren during summer. On the 160 acre rodent study area, for instance, only four were found, along with 63 gopher snakes and 273 rattlesnakes.

The local population of this snake belongs to the California king snake, *Lampropeltis getulus californiae*. Only one of those examined had some slight tendency to longitudinal elongation of the markings in the ringed pattern. This tendency culminates in the striped pattern phase common in extreme southern California. In adults, especially the females, dark markings were often chocolate brown, rather than black as in populations farther north.

General behavior.—As with most other reptiles of the Range, king snakes were found mainly in the spring months; 35 of the 43 total were recorded in April, May or June. Many were found when they were crossing roads. They

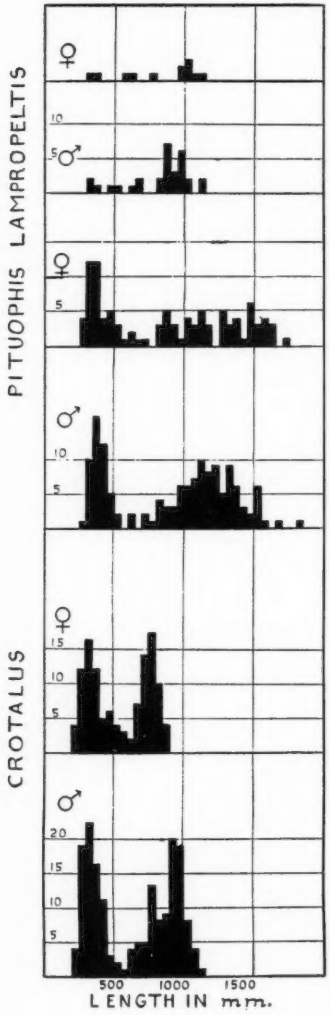

Fig. 10.—Size groups of rattlesnakes, gopher snakes, and king snakes, showing sexual differences, and relative abundance of young and adults; 1940 data only included for rattlesnakes.

are of somewhat secretive habits. Though slow-moving, they were usually near cover, into which they were quick to escape. In motion, the ringed pattern blends into the background making the snake difficult to see when it is moving under cover. When put on the defensive, a king snake would sometimes hide its head beneath its coils, shifting about in nervous, jerky fashion when it was touched. Others would make short strikes but usually without attempting to bite. Such cornered snakes would usually vibrate their tails, and would evert their anal glands, sometimes coiling and smearing their own bodies with the secretion.

On one occasion a large adult climbed up on the 3½ foot wall of an outdoor concrete pit in which several rattlesnakes were confined, and was apparently watching them, but it did not enter the pit.

In May 1946, mating behavior was observed when several king snakes were held in confinement for a few days. A male would glide over the female, with chin pressed against her back, and would grasp her body anteriorly in his jaws. Two males were confined together in a small cage. After several days, when they were released, the smaller showed evidence of having been attacked, bitten and constricted. Over large areas of its body the scales were roughened with numerous small lacerations, and it moved feebly as if partly paralyzed. It was later found dead near the point of release. If encounters between rival males during the breeding season occur in Nature, it is doubtful whether they would be continued to the point of death or serious injury before the attacked snake escaped.

TABLE 24.—Growth in king snakes.
(All adult males)

Months elapsed between captures	Length gain in mm.	Weight gain in grams
75—	978 to 1160	229 to 595
74+	885 to 1118	268 to 488
72+	920 to 1050	216 to 315
24—	1036 to 1055	306 to 430
13—	989 to 989	313 to 315

Growth.—Only six of the 43 recorded were less than 500 mm. in length, probably young of the year. This represented 14 percent as against nearly 30 percent of young in the gopher snake population and 22 percent in the rattlesnake. The king snake may have smaller broods with greater survival expectancy at the time of hatching; secretive tendencies in the small young may also be involved. Seven of the king snakes recorded were somewhere between small young and adult size; this half-grown group was more numerous than small young, whereas in both gopher snake and rattlesnake small young of the year greatly outnumbered those that were partly grown. Klauber (1939: 13 and 22; 1944: 87) records San Diego County broods hatched in captivity with the following numbers: 7 with 7, 4 with 4, 3 with 6, and 2 each with 10, 9, 8, 5, and 1 young. These broods average 6.1 young, a smaller number than the usual brood of the rattlesnake or gopher snake, however, the actual clutches laid were somewhat larger, as there was some loss during incubation.

None of the young king snakes marked was among those recaptured. In all, eleven marked king snakes were recaptured after intervals of from four days to more than 6 years. Several made substantial growth.

These records show gradual increase in length and weight after adult

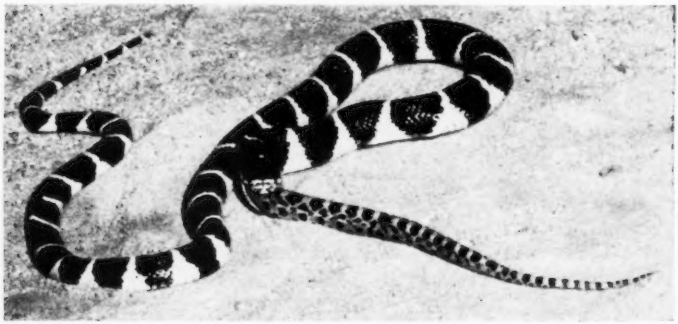

Fig. 11.—King snake swallowing a gopher snake of almost equal length.

size has been attained. Of the few marked, four were recaptured after intervals of more than 6 years, suggesting a high survival expectancy after adult size is attained.

Movement.—Ten of the king snakes marked and recaptured had moved distances indicated in Table 25.

TABLE 25.—Distances between points of capture of marked king snakes.

Distance in feet between points of capture	Number of months elapsed between captures	Age and sex
1840	1—	adult ♂
1800	1+	adult ♂
960	75—	adult ♂ (3 captures; one each in '39, '40 and 46)
900	24—	adult ♂ (5 captures; one in '38, one in '39, three in '40)
790	72—	adult ♂
660	1—	adult ♂
600	13—	adult ♂
580	2—	subadult ♀
380	74+	adult ♂ (3 captures; 2 in '40, one in '46)
150	(4 days)	subadult ♀

These records demonstrate permanent residence in small areas of favorable habitat, only a few hundred yards at most in longest diameter. In general, the movements are of about the same magnitude recorded for gopher snakes, but king snakes either are less inclined to wander, or they have a greater survival expectancy. Four marked survivors of the pre-war study were recaptured in the headquarters area in 1946 and 1947, while none of an originally more numerous group of marked gopher snakes was recaptured on the area after this interval.

Feeding.—Only five instances of king snake feeding were recorded, three in June, one in July, and one in October. One adult male was found on a quail nest which it had just robbed. Along with seven eggs from the nest it contained remains of a harvest mouse. Another adult male contained several quail eggs but digestion was so far advanced that the number could not be determined. Another adult male contained a whiptail lizard. One was found in the process of swallowing a gopher snake of proportionately large size (Figure 11). A young (401 mm.) female was found in the process of constricting a skink. For ten minutes that it was observed from a distance, it lay in a compact enveloping coil making hardly any movement. When the observer approached, the snake relaxed its grip, and the skink taking advantage of its momentary respite, ran unsteadily to a nearby hole and escaped.

These few records are insufficient to provide a clear idea of the king snake's diet, but their trend differs from those of the rattlesnake and gopher snake. Reptiles perhaps make up the greater part of the food, supplemented by eggs, with mammals of only minor importance.

Natural enemies.—Ten king snakes were recorded among 4110 vertebrate prey items of the red-tailed hawk, and were calculated to comprise about one-fourth of one percent of the weight of recorded prey, assuming an average adult weight for each recorded item. Among the 625 nest prey items of the hawks there were no king snakes, although this was at the season when the snakes are most active. Among 968 vertebrate pellet prey items of the horned owl, there were two king snakes. Twice king snake remains were definitely identified among a total of 1924 vertebrate prey animals in coyote scats. Fourteen other occurrences listed merely as "snake" may have included others of this species which had no readily distinguishing features to identify it from poorly preserved scale and bone fragments in scats. In the combined totals of prey records for various predators the ratio of king snakes to gopher snakes is low; 14 to 307. Even in view of the greater abundance of gopher snakes, the records of predation on the king snake are relatively few. This concurs with the idea that it is relatively safe from natural enemies, and has a slower population turnover.

The king snake's preferences for situations where sheltering thick vegetation is at hand, and its readiness to take advantage of such cover, may in part account for its success in eluding predators.

GARTER SNAKE

Thamnophis elegans couchii

The two species of garter snakes on the Experimental Range are much different both in habits and in superficial appearance. *T. e. couchii* is dull brown, while *T. o. tetrataenia* is gaudily colored. The local population of the former is somewhat intermediate between typical *couchii* and the San Joaquin Valley race *gigas*. It lacks the characteristic facial pattern, and the well defined checkered pattern of typical *couchii*, having instead the overall muddy brownish color of *gigas*, though not having the 23 dorsal scale rows nor the large size typical of that race.

General behavior.—In a revision of the group (Fitch, 1940) it was demonstrated that garter snakes of this subspecies and closely related ones are specialized in their adaptation to aquatic life, and are generally found in or near permanent streams. Subsequent findings at the Experimental Range (Fitch, 1941) indicated a wider range of tolerance for drought conditions than had been recognized before, since most of the foothill streams, supporting abundant populations, went dry in early summer. During the hot, dry months of summer and early fall the snakes were rarely seen, even in the streamside situations where they abounded in late March, April, May and early June. In

two small reservoirs where water remained, a few were in evidence throughout the summer, but there were no striking concentrations. Evidently most of the garter snake population remained through the dry season in the vicinity of creek beds, but became much less active, prowling in the sheltered, damp situations where amphibians might be found.

Feeding.—At this locality amphibians evidently provide the staple food source, and they comprised all the items recorded for this species of snake. Those identified included: 10 California toads, 2 tree-toads, and 1 spadefoot toad (all newly metamorphosed), 70 tadpoles of the same three species, and 2 larval tiger salamanders.

Growth.—A total of 97 snakes of this species were marked and released, 67 in 1938, 8 in 1939, and 22 in 1940. Eight were recaptured. The five of these recaptured after substantial intervals (all females) had made the gains in head-and-body-length indicated in Table 26.

TABLE 26.—Growth in garter snakes.

Months elapsed between captures	Head-and-body-lengths in mm.
24+	615 to 640
12+	790 to 795
11+	750 to 787
8+	570 to 570
8—	210 to 442

Those of adult size grew slowly or failed to make any gain, while the one small young made remarkably rapid gain, from 210 to 442 mm. in the period September 16, 1938 to April 24, 1939. It may have been unusually accelerated, as some collected in late spring were still under 300 mm. in length.

Seibert and Hagen (1947) found that in first-year plains garter snakes (*Thamnophis radix*) marked by them, the average rate of growth amounted to a gain of .45 inches per week. They believe that some of the second-year females were gravid. For the plains garter snake the growing season is shorter, and adult size is smaller than in the present form.

Breeding in *T. e. couchii* probably occurs in early spring, and the newborn young may appear in late July, considerably earlier than the young of other local snake species. They then have as much as three months for feeding and growth before entering their first hibernation.

In this species, as in other natricines, females attain larger size than males; size groups of the two sexes in Table 27 illustrate this.

Movement.—These snakes evidently move more extensively than the other species studied. None of the many marked along several hundred yards of

TABLE 27.—Size and sex groups of *Thamnophis elegans couchii*.

Head-and-body-length in mm.	Males	Females	Undetermined
201 to 250	7	5	2
251 to 300	2	4	
301 to 350	1	7	
351 to 400	4	3	
401 to 450	5	6	
451 to 500	7	6	
501 to 550	10	4	1
551 to 600		8	
601 to 650		5	
651 to 700		1	
701 to 750		1	
751 to 800		3	
801 to 850		1	
851 to 900		1	

the creek within the rodent study area was ever found there again, although the part of the creek where they were found was followed hundreds of times subsequently. If any had stayed in the vicinity, they almost surely would have been recaptured, as they spend much time in the open, and stay near the water, prowling from pool to pool along the creek beds. Of the few marked ones recaptured, several had moved long distances.

Seibert and Hagen (1947) studying the plains garter snake in Illinois, marked 298 on an area of 3.2 acres (in a strip 390 yards long). They recaptured 41 the same season, and of these 19 had moved less than 30 feet, 11 more moved less than 90 feet, 10 more moved less than 300 feet, and only one moved more than 300 feet. The extreme localism of these plains garter

TABLE 28.—Distance travelled by marked garter snakes.

Distances in feet between points of capture	Number of months elapsed between captures	Age and sex
5550	12+	adult ♀
4950	8—	young ♀
1920	8+	adult ♀
300	11+	adult ♀
240	24+	adult ♀
100	1+	adult ♀
100	[11 days]	adult ♂
no movement	[7 days]	subadult ♀

snakes evidently was correlated with their type of habitat, with dense ground cover and abundant hiding places.

Natural enemies.—The California heron, though not resident on the area, comes in numbers in the spring when the shallow creeks are teeming with tadpoles. It may be the most destructive enemy of this kind of snake. The raccoon and skunk also may take many, but the feeding of these two predators was not investigated. Among 4110 nest and pellet vertebrate prey occurrences of the red-tailed hawk, there were only 4 garter snakes, and they were not represented at all among 968 vertebrate prey items of the horned owl, nor among 1924 vertebrate prey items of the coyote. The repellent anal scent may be effective protection against some of these predators, which eat other kinds of snakes.

GARTER SNAKE
Thamnophis ordinatus

The form of the common garter snake (*Thamnophis ordinatus tetrataenia*) on the Range is distinguished by its bright yellow dorsal stripe, and crimson lateral marks on a black ground color; it is by comparison, much scarcer and more localized on the area than is *T. elegans*. A total of 24 were recorded, and most of these were in the vicinity of headquarters where the water supply in two small reservoirs, and moisture in a large swale provided suitable habitat conditions during most of the dry season.

Three of those marked were recaptured. One of unusually large size marked in June 1938 was recaptured in March 1939, and again in March 1941, and its length had increased from 875 to 911 mm. with corresponding increase in tail length and weight; all three records were within a 660 foot diameter. Another large female moved 400 feet in a little more than two months; the third had moved 2640 feet in 20 days.

Only two feeding records were obtained. One large one was found trying to swallow an adult toad. Another voided feces containing mammal hair, probably that of a meadow mouse.

CALIFORNIA RACER

The California racer (*Coluber lateralis*) usually avoided capture by its speed and wariness. Twenty-six were marked and released, mostly in 1938, but none was recaptured. Young of these racers were not often seen, and none was secured for measuring. Racers recorded were of the following size groups: 600 to 700 mm.—1; 700 to 800 mm.—3; 800 to 900 mm.—5; 900 to 1000 mm.—14; 1000 to 1032 mm.—3.

General behavior.—This chaparral-haunting species was nearly always seen in the vicinity of manzanita or ceanothus thickets into which it climbed to escape. Sometimes, at an alarm, one would dart through a bush to its farther side, and lie motionless there until closely approached. In such situations they

were difficult to see. Another escape reaction consists of darting away with a violent lateral thrashing, causing a commotion that draws attention, then gliding back silently to the point where it had started, where an enemy might be least likely to look for it.

Each of three racers had an adult skink in its stomach, each of two others had eaten an adult meadow mouse and another a whiptail lizard. One July morning several orioles and blackbirds were noticed in willows and low weeds scolding at a central object in a thick clump. Distress calls and fluttering revealed that a racer had caught a fledgling Bullock oriole by the leg, but it became alarmed, released the bird, and darted away.

Probably this slender-bodied snake finds most of its subsistence in the abundant lizard populations, with young birds of secondary importance. Racers may sometimes prey upon young rattlesnakes in this locality, as they are known to do elsewhere (Van Denburgh, 1922: pl. 69).

Natural enemies.—Many records of destruction of the California racer by various predators were obtained, as follows:

Red-tailed hawk	50 occurrences among	4110 items
Horned owl	7 occurrences among	968 items
Coyote	7 occurrences among	1924 items

SPOTTED NIGHT SNAKE

This snake belongs to the recently described subspecies *Hypsiglena ochrorhyncha nuchulata* (Tanner, 1943). Dunn (1936) and Bogert and Oliver (1945: 381) have expressed the opinion that *ochrorhyncha* intergrades with the Mexican species *torquata*, and its taxonomic status is perhaps still unsettled.

This small, secretive snake was found under boulders of granite outcrops. In the spring of 1938, when boulders were moved to build a rock wall, numbers of the snakes were found within a small area, suggesting that it may be actually abundant though seldom seen.

Night snakes displayed a curious defense reaction, greatly flattening the head and body and coiling in a tight spiral with the head on top. From this position one would make short, poorly aimed lunges, which might be continued several seconds after the annoying object had been removed.

Of those found, only one contained food, a young fence lizard. Published records indicate that the species is mainly saurophagous, and that the prey is subdued by the venomous bite.

LONG-NOSED SNAKE

The secretive and nocturnal habits of the long-nosed snake (*Rhinocheilus lecontei lecontei*) render encounters relatively infrequent. The fact that it was not found more often during the course of prolonged and intensive field work, including hundreds of miles of night driving, indicates that it is by no means

common locally. It was recorded four times, once as prey in a red-tailed hawk nest, once as a dried carcass found in open grassland, once under a log in a pile of granite boulders, and once crossing a road at dusk. The one found beneath the log had in its stomach a large adult skink, weighing 18 grams. The skink's tail was newly broken, evidently by the snake.

RING-NECKED SNAKE

Only two individuals of the ring-necked snake (*Diadophis amabilis amabilis*) were found on the Range, and nothing was learned concerning its habits in this region.

DISCUSSION

Of the nine snake species that occur on the San Joaquin Experimental Range, only two were found to have sufficiently high populations and predatory habits to render them important in the economy of the region. These were the rattlesnake and gopher snake. The long-nosed and ring-necked snakes are actually rare. The remaining species are limited in numbers and distribution by habitat specializations; the racer to chaparral, the two kinds of garter snakes to the vicinity of creek beds where there is water during at least part of the summer, the night snake to larger granite outcrops or rock piles, the king snake to an area of rank vegetation where swale moisture remains in the summer. There are also specializations in feeding habits; garter snake predation is directed almost entirely at the amphibian populations —in the absence of fish in these intermittent foothill streams—though *T. ordinatus* may take an occasional rodent or lizard. The racer is an actively prowling and climbing species that evidently lives mainly on the larger lizards, varying its food with an occasional bird or rodent, and possibly with small snakes or even insects. The night snake and long-nosed snake probably live mostly on lizards, and the former may be common enough to affect their populations. The king snake seems to subsist principally on reptiles, both snake and lizard, but takes some rodents and birds' eggs. Its habitat preferences are similar to those of the valley quail, and the fact that two of five that contained food had eaten quail eggs suggests it may be one of the important nest predators of this game bird in certain limited areas.

Only the rattlesnake and the gopher snake are primarily rodent predators. They are similar in feeding habits, and for the young of each lizards are an important part of the diet. However, gopher snakes, unlike rattlesnakes, also eat birds' eggs, whereas young rattlesnakes eat spadefoot toads, which are not taken by the gopher snakes. Attempts to census rattlesnakes by ratio of repeats among those taken on limited areas yielded such variable results with different sets of figures that numbers cannot be accurately stated, but allowing for the extensive individual prowling range (apparently one-sixth to one-fourth mile in diameter) it appears most probable that the population is roughly 1.2 rattlesnakes per acre on the 80 acre area where intensive sampling was attempted. It is uncertain whether this area is representative of the entire Experimental Range since it is relatively open, with less rock and brush, and

has a comparatively high ground squirrel population, but fewer kangaroo rats and cottontails than other areas. It is probable that rattlesnakes are fully as abundant on most other parts of the Range, with the exception of the headquarters area. After riding the Range for nearly twelve years, Kenneth A. Wagnon was of the opinion that the rattlesnake population was not noticeably concentrated on any particular areas, but that the average size was larger on the more remote portions where they were subject to least disturbance and killing by man. Gopher snakes were found in a ratio of one to 3.7 rattlesnakes, and if this is accepted as an index to their actual numbers, a population of about .3 per acre is indicated.

The amount of prey taken depends on the sizes of the snakes as well as their numbers. The average weight of rattlesnakes taken during the spring season of greatest activity in 1940 was slightly more than 200 grams, and if each snake ate twice its weight annually (a probable minimum figure if the amounts consumed by those kept in confinement are typical) the quantity of prey eliminated annually would probably approximate 420 grams per snake. The 1.5 snakes per acre comprising the combined rattlesnake and gopher snake populations would, on this basis, account for a prey weight of 630 grams, or about 1.4 pounds annually. Expressed separately for each of the common prey species, this would amount to two or three young ground squirrels or cottontails, ten adult kangaroo rats, or the same number of young gophers or woodrats, 32 white-footed mice, or 52 adult pocket mice or whiptail lizards. In the proportions represented by the actual food samples, the toll of prey would be about as follows:

Ground squirrel (1/3 grown)	nearly two to 1	acre
Cottontail (small young)	one to 2	acres
Woodrat (half-grown)	one to 1	acre
Kangaroo rat (adult)	one to 2	acres
Pocket mouse (adult)	one to 3	acres
Pocket gopher (2/3 grown)	one to 3½	acres
Mouse (*Peromyscus* or half-grown *Microtus*)	one to 1	acre
Lizard (small adult fence lizard or skink)	one to 2	acres

The effect of this predation on the prey species depends on the population density and the reproductive rate of each kind. The ground squirrel occurred in breeding populations of about 1½ per acre, and its estimated annual increase is about five per acre (the breeding population consists of about 55 percent females, each producing one litter annually averaging seven young). The snakes' toll would amount to perhaps forty percent of the annual increase, if the spring food sample were representative of the feeding throughout the year. But probably predation on ground squirrels is much reduced or discontinued during the latter half of the season. Kangaroo rats and other rodents may be substituted. Any squirrels taken during the late summer months must be well grown ones, which are therefore required in smaller numbers to satisfy the food requirements of the snakes.

Cottontails occurred in summer populations computed as .8 per acre in

1939 and .4 per acre in 1940 on the 80 acre study area, but they were more common on other parts of the Range. Orr (1940: 143) has stated that the Audubon cottontail produces two or three litters annually with an average of 3.6 per litter, which would amount to about nine young per female and females may reach maturity and breed at an age of six months, indicating an even higher reproductive potential through the production of more than one generation annually. An average of 1.7 to 3.7 young per acre would be produced by the 1940 and 1939 populations. The one young per two acres eliminated by snake predation would constitute an important part of the annual reproduction but actually the predation on rabbits recorded in the sample probably takes place only in spring, so that perhaps considerably less than half the computed rabbit weight would actually be eliminated.

The reproductive rate of the kangaroo rat is uncertain as the species breeds throughout most of the year, with a peak in April, tapering off to almost complete cessation in late fall and early winter. Young a few months old are known to breed, so that two or more generations can be produced annually, and adult females may normally produce two or more litters with an average of 3.7 young per litter (Tappe, 1941: 146; Fitch, 1948a: 21). With this rapid population turnover, and high reproductive potential, it might be expected that the annual production would amount to at least 15 or 20 young per acre. At this rate, the annual toll of one for two acres estimated for the rattlesnake and gopher snake would have little effect. If in the latter half of the season, kangaroo rats were substituted for that portion of the diet made up by rabbit and squirrel during the spring period represented by the feeding sample, several per acre would be consumed, perhaps a substantial part of the annual increase. However, the kangaroo rat population undergoes irregular fluctuations over periods of years that are obviously not related to snake predation. At times when the maximum population is attained—perhaps 30 or more per acre—snake predation would have little effect, but when reduction occurs to a low point, of only one per acre as in 1946, the survivors might be unable to hold their own unless such predators were largely diverted to more readily obtained prey.

The pocket gopher normally occurs in even higher populations than the kangaroo rat, and having a comparable rate of reproduction, is adapted to withstand severe predation pressure. However, insofar as determined, the extent of snake predation on the gopher locally is so slight as to be negligible in the ecology of either predator or prey.

In contrast with the associated predatory mammal and bird species, snake populations occur in remarkably high concentrations, for example 120 rattlesnakes to a horned owl, 190 to a red-tailed hawk, and several hundred to a coyote on a range where each of these species might be considered abundant. Factors that favor such concentrations are their relatively small size, physiological characteristics permitting existence on relatively small quantities of food with long fasts intervening, and general lack of intraspecific intolerance. An average sized rattlesnake would weigh only one-fifth as much as a red-tailed hawk, or one-sixtieth as much as a coyote. Its annual food require-

ment would provide enough for the hawk for only a few days, or would scarcely furnish one adequate meal for the coyote. Snakes ordinarily behave toward members of their own species as toward inanimate objects. The complex social patterns involving territoriality and dominance that appear in many higher vertebrates are lacking.

Recent studies by Lowe (1948), Shaw (1948), and some earlier workers indicate that at times active struggles for dominance occur between the adult males of certain kinds of snakes, including rattlesnakes and other pit vipers. As yet adequate accounts of such encounters under natural conditions are lacking, and their significance is not entirely clear. Success in vanquishing a rival in such contests may lead to success in mating. A possible instance of this was recorded early in the present study, when a large adult male rattlesnake was found dead, with post mortem evidence of snake bite, only ten feet away from a mating pair of the same species (Fitch and Glading, 1947: 121). It seems obvious that the occurrence of such encounters does not constitute territoriality in the sense in which it occurs in certain birds and lizards, for instance. In such forms, occupancy of an area by an individual or pair may preclude the uncontested presence of any other member of the species. The pressure of intraspecific strife then constitutes a limitation on the numbers which may successfully exist on any given area.

The food supply is, however, the factor which must ultimately limit snake populations. The presence of many different prey species assures a reliable and constant food supply, even in the periodic or seasonal scarcity of any one kind. Also, it assures food for snakes of all sizes since certain prey species are taken almost exclusively by the young, and others almost entirely by well grown snakes. Just how the food supply limits the population or affects the individual snake is not entirely clear. The chances of any one snake obtaining food must be proportional to the number of prey animals on the area where it prowls. That actual starvation does occur at times, seems probable. Adult snakes were not in uniformly good condition and some were thin. A critical shortage of food might affect the adults by decreasing their productivity rather than by outright starvation. Young were found that were actually emaciated, and in weakened condition. They are handicapped both in having a narrower range of prey species than adults, and lacking the reserve of stored fat. Food shortage probably results in more prowling in exposed places, leading to higher losses to predation, especially since the snakes are eaten by the same predators that compete with them for prey. Snakes are relatively long lived as compared with their prey species, or even with their associated bird and mammal predators. One may outlive many generations of its rodent prey, and survive drastic changes in their numbers. In contrast with predators of other types, which may respond to reductions in their prey populations by shifts to new areas, or may soon be reduced to starvation, snakes seem relatively insensitive, and are better able to weather years of scarcity. Therefore they might have more stabilizing influence, especially on reduced prey populations, than have those predators in which numbers follow the population cycle of a prey species, lagging behind its changes. But, of course, they are not able

to concetrate in areas of prey abundance as rapidly as do bird and mammal predators.

Whether snake populations have any important effect in controlling their prey populations is debatable. The available figures seem to indicate destruction of a substantial part of the annual increase for several of the more important rodent and rabbit species on the range. Snake predation alone apparently would be a minor factor in its effect on these prey populations, but combined with that of hawks, owls, foxes, and coyotes, each taking similar quantities, it would add up to a major part of the annual surplus, at least for the cottontail, ground squirrel, kangaroo rat, and woodrat. There are no evident compensatory factors, such as critical food shortage or intraspecific strife, that would be apt to function as substitutes for predation in eliminating the same percentages of the rodent crop in their absence. Therefore, it seems fairly certain that if the predator populations of the Experimental Range were eliminated, the ground squirrel, cottontail, kangaroo rat and woodrat populations might advance to somewhat higher average levels.

Any appraisal of the economic status of snakes in the foothill ranges must take into account the damage done to man and his domestic animals by the rattlesnake through its venomous bite. During the course of the present study a total of five rattlesnake bites were sustained by the writer and three of his co-workers as a result of improper handling. Otherwise, no cases of rattlesnake bite were recorded on the Range or surrounding ranches, although hundreds of persons worked in the field for varying periods and many "narrow escapes" were reported, sometimes involving actually stepping upon a rattlesnake by a person unaware of its presence.

Grazing livestock are often exposed to snakebite. Wagnon, Guilbert and Hart have written (1945: 18) ". . . cattle will usually recover without treatment. Cattle are not afraid of rattlesnakes even after having been bitten. . . . at present snake bites seem to be an unavoidable minor source of loss on ranges where snake infestations are heavy." The same authors (1946: 13) stated that the annual incidence of snake-bite in the Experimental Range herd averaged 1.9 percent. During an eight year period for which records are available, the experimental herd increased from an annual maximum of 124 to 264, and usually averaged about one animal to 20 acres for the 4600 acres of the Range (until excess animals were marketed in July and August). Under these conditions, and with an estimated 1.2 rattlesnakes per acre, 34 bites and seven deaths were recorded in the herd for the eight year period. Of the cattle bitten, 29, including all seven of those that died, were injured about the head and neck. Three were bitten on the limbs, one on the udder, and one on the brisket. Those that died included three steers, two heifers, one calf, and one adult cow. The bites were fairly evenly distributed over the years as follows: six in 1936; two in 1937; three in 1938; six in 1939; four in 1940; four in 1941; four in 1942; four in 1943. In some instances effects of the bite passed rapidly, so that the value of the animal was not impaired; but in others there was persistent swelling, abscesses developed, and weight losses were severe.

SUMMARY

Nine species of snakes are known to occur on the San Joaquin Experimental Range in the woodland foothill belt of central California. In their approximate order of abundance, these are: Pacific rattlesnake (*Crotalus viridis oreganus*), Coast gopher snake (*Pituophis catenifer catenifer*), spotted night snake (*Hypsiglena ochrorhyncha nuchulata*), California racer (*Coluber lateralis*), garter snake (*Thamnophis elegans couchii*), California king snake (*Lampropeltis getulus californiae*), garter snake (*Thamnophis ordinatus tetrataenia*), western long-nosed snake (*Rhinocheilus lecontei lecontei*) and western ring-necked snake (*Diadophis amabilis amabilis*). Many snakes were marked by scale clipping for further identification, including 679 rattlesnakes, 256 gopher snakes, 121 garter snakes (97 *couchii*, 24 *tetrataenia*), 44 king snakes, and 26 racers. Substantial percentages of these were recaptured after intervals of from a few hours up to nearly nine years, and facts regarding their movements, growth, rattle development (in the rattlesnake), populations, and survival were revealed. Among 156 rattlesnakes a total of 203 recaptures were made; with 31 gopher snakes there were a total of 33 recaptures; with 11 king snakes a total of 16, and with 11 garter snakes a total of 14.

Though differing in many other respects, all species were similar in their seasonal schedule of activity, hibernating typically from about mid-October to mid-March and appearing in greatest numbers in a period of weeks following emergence from hibernation, in April and May. More than 400 feeding records obtained represent this spring period disproportionately and hence are of doubtful validity in showing the year-round feeding habits.

The rattlesnake population sample obtained in spring was found to consist of more than half adults, with young of the year making up a little more than one-fifth of the total. The adult population consists of an accumulation of survivors of many successive annual age groups, as only a small fraction of the numbers in each annual brood attains adult size. Heaviest losses are sustained during the first year, when predation, various accidents, and probably starvation, eliminate many. Growth in young rattlesnakes is variable. In some, the stunting effect of handling and marking tended to obscure the trends. Also, many of the less thrifty young make little or no growth over periods of months, and probably often succumb, so are not representative of development in the minority that attain adult size. The young are born in fall and make most rapid growth just before and just after the first hibernation. At an age of 18 months in spring after emergence from the second hibernation they may have grown to approximately 500 mm. in head-and-body-length, an increase of some 220 mm. over the original length. For the first year an average gain of some 24 mm. for each active month is indicated. At an age of three years they have usually attained small adult size of somewhat more than 700 mm., but may continue to grow for many years. Four years or more ordinarily would be required to reach average adult size. At all stages rate of growth varies greatly between individuals. Rate of rattle development also is unpredictable, although probably less so than growth in length. Young generally add a second rattle to their original button in early summer

following their first hibernation, and, at the age of a year, are apt to have a string of four rattles including the button. Fifth, sixth, and seventh rattles are often acquired in the second growing season. Adults gain approximately 1.5 rattles annually in males and 1.1 in females.

Numerous records of the distances traveled by individual rattlesnakes between captures did not demonstrate any stereotyped pattern as to range of activities or rate of movement. But in those for which records over periods of months or years were obtained, male ranges of nearly a quarter mile in diameter, and female ranges of about one-sixth mile in diameter appeared to be most typical. Several were recorded to have moved more than a mile, and a greater number had moved more than half a mile, but in the majority of instances snakes were found after long periods of months or years within a few hundred feet at most from the point of release. This held true even in instances of release at a distance from the point of capture. In a group recaptured in 1946 and 1947 after lapses of five to nine years, nearly all were in the general vicinity where they had been released, indicating limitation to small prowling ranges even though some made more extensive movements in short periods. These were mostly adults. Young are less attached to definite areas as shown by the fact that each year numbers of them wandered into the headquarters area of the Experimental Range, where adult rattlesnakes had been killed off.

Census computations on the sampling area of 80 acres, based on the ratio of recaptures among the rattlesnakes taken, yielded variable figures. For several such censuses combined, a figure of approximately 1.2 per acre was obtained, after allowance was made for extent of individual ranges outside the 80 acres boundary.

The gopher snake was found less frequently than the rattlesnake, in a ratio of 1 to 3.7; if this ratio is representative of its actual numbers, it may occur in a population density of about .3 per acre. As compared with rattlesnakes, gopher snakes make more rapid growth, proportional to their larger adult size. They reach maturity just as soon, or perhaps sooner. Gopher snakes, like rattlesnakes, are attached to limited areas of a few hundred feet in diameter, at most, and remain in such areas over long periods of years.

King snakes are relatively scarce on the Range, and are largely confined to an ungrazed swale area having persistent summer moisture and a rank growth of annual vegetation. Apparently their movements are even more limited than are those of rattlesnakes or gopher snakes, and the ratio of recaptures was high among the few that were marked.

Garter snakes were found to be limited to the small intermittent creeks on the area. No information on their numbers was obtained. The percentage of recaptures was low, and the distances covered between captures averaged high, indicating that garter snakes wander far more extensively than the other kinds, evidently following the watercourses.

The food preferences of the rattlesnake and gopher snake are similar, but methods of hunting differ. The rattlesnake lies in wait, at burrow entrances, along trails, or in other strategic places, strikes animals coming within reach,

and then attempts to track them down after death, but often fails to find them. The gopher snake prowls more actively and often hunts out the prey in its nest. Estimated percentages, by weight, of the rattlesnake diet from a sample of 285 items, representing mostly the spring season, were as follows: ground squirrel 68.8%; cottontail 17.3%; kangaroo rat 5.5%; pocket gopher 2.5%; woodrat 1.7%; and six species of mice, four of lizards, chipmunk, quail, towhee, spadefoot toad, each less than one percent. It is likely that during summer and early fall, a season for which few records are available, feeding is largely diverted from ground squirrels and cottontails, then too large to be swallowed by most snakes, to kangaroo rats.

For the gopher snake approximate percentages by weight of 71 recorded food items (omitting the record of one unusual item, an adult cottontail) were: ground squirrel 44.3%, woodrat 29.5%, cottontail 19.7%, quail egg 8.4%, pocket gopher 6.4%, mouse (*Peromyscus*) 4.5%, meadow mouse 3.4%, fence lizard 1.5%, kangaroo rat 1.3%, pocket mouse .6% and brown-shouldered lizard .4%. For king snakes only six feeding records were obtained: two clutches of quail eggs, a gopher snake, a whiptail lizard, a skink, and a harvest mouse. Garter snakes were found to have fed almost entirely on amphibians, mostly tadpoles of the tree-toad, spadefoot toad, and California toad, though one (*T. ordinatus*) had eaten a small mammal. Seven prey records were obtained for the California racer: three skinks, two meadow mice, one whiptail lizard, and one fledgling oriole. The latter, however, escaped the racer that attacked it, when an observer intervened. A night snake had eaten a young fence lizard, and a long-nosed snake had eaten an adult skink.

The rattlesnake and gopher snake populations computed at roughly 1.2 and 0.3 snakes per acre, respectively, were found to have an average weight of nearly half a pound per snake. Each snake must consume annually a prey weight of at least double its own weight. The toll of rattlesnake and gopher snake predation combined would eliminate a prey weight of perhaps 1.4 pounds annually for each acre, on the average. This predation pressure is distributed among many species, but with the ground squirrel and cottontail absorbing fully 85 percent of it, in spring and early summer, at least. There is some evidence that the kangaroo rat bears the brunt of predation during late summer and early fall, though few records are available for that season. The actual number of prey animals destroyed would depend upon the proportions made up by the different species taken, and the stage of development of each. However, snake predation apparently would eliminate a small but substantial part of the annual increase of ground squirrels, cottontails and kangaroo rats—three of the species most important as destroyers of range forage.

Rattlesnakes do some damage to domestic stock. On the seven square miles of the Experimental Range stocked with cattle at the rate of about one head to 20 acres, over an eight year period, seven deaths and a total of 34 snake bites were recorded. In some instances recovery was rapid, but in others, bitten animals suffered severe weight losses entailing financial loss despite their eventual recovery.

Various predators were found to have eaten snakes, several kinds of which were revealed in scat and pellet examinations, and at nests of raptors. The predators which ate snakes and their total numbers of recorded prey items and of each snake species are shown in Table 29.

Many other kinds of local predators probably eat snakes, but only those kinds known to be important rodent destroyers were investigated. The California heron comes in numbers during the spring, and probably is an important enemy of garter snakes, since it hunts in the same places where these snakes are found. The roadrunner may be one of the most important natural enemies of snakes. It is fairly numerous, but its feeding habits were not investigated and the three records of predation on rattlesnakes were obtained by chance. The gopher snake occurred much oftener than the rattlesnake in extensive prey sample of red-tailed hawk, horned owl, and coyote although actually less common, reflecting its higher rate of reproduction and population turnover, and also the instinctive caution of predators towards the dangerous rattlesnake.

TABLE 29.— Predation on snakes by bird, mammal and reptile predators.

Kind of predator	Total vertebrate food items recorded	Number of snake occurrences in food items							
		Rattlesnake	Gopher snake	King snake	Racer	Garter snake	Long-nosed snake	"Snake"	"Reptile"
Red-tailed hawk	4110	74	204	10	50	4	1	43	32
Horned owl	968	4	20	2	7	—	—	4	1
Barn owl	517	—	1	—	—	—	—	—	—
Roadrunner	—	3	—	—	—	—	—	—	—
Cooper hawk	42	1	—	—	—	—	—	—	—
Coyote	1924	17	79	2	7	—	—	19	1
Gray fox	102	—	2	—	—	—	—	—	—
King snake	6	—	1	—	—	—	—	—	—

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The Genera of Gerrhonotine Lizards[1]

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Introduction

The term "gerrhonotine lizards" is used throughout this paper to include all Recent Anguidae with four well-developed limbs and a lateral fold. Thus defined, it constitutes a distinctly delimited assemblage of somewhat over forty forms, ranging from British Columbia to Panama. It is largely for the sake of a convenient name to designate this group that the term "gerrhonotine lizards" or "Gerrhonotinae" is used. Whether or not the group actually deserves subfamily status can be determined only by a comparative study of greater scope than is feasible for the present writer to undertake at this time. *Ophisaurus* among modern genera and *Peltosaurus* and *Melanosaurus* among the fossil forms show rather close affinities to the gerrhonotine group, but I have not considered them in the present discussion.

This paper deals only with the generic relationships within the group. A discussion of relationships at lower levels, and descriptions of individual forms, are reserved for treatment elsewhere.

Acknowledgements

I am deeply indebted to Dr. Sherman C. Bishop of the University of Rochester and Dr. Hobart M. Smith of the University of Illinois for their many helpful suggestions and criticisms during the course of my study and the preparation of this paper, also to Dr. E. R. Dunn of Haverford College and Drs. Norman Hartweg and L. C. Stuart of the University of Michigan. The following individuals have been very generous in granting me the loan of personal specimens, or specimens under their care in the institutions with which they are connected: Dr. Doris M. Cochran of the U. S. National Museum, Mr. Charles M. Bogert of the American Museum of Natural History, Mrs. Helen T. Gaige and Dr. Norman Hartweg of the University of Michigan, Dr. Edward H. Taylor of the University of Kansas, Mr. Karl P. Schmidt of the Chicago Natural History Museum, Dr. E. R. Dunn of Haverford College, Dr. Rafael Martín del Campo of the Instituto de Biología of Mexico, Mr. R. T. Moore of the California Institute of Technology, Mr. Arthur Loveridge of the Museum of Comparative Zoology, Dr. A. H. Wright of Cornell University, Mr. M. Graham Netting of the Carnegie Museum, and Dr. Angus M. Woodbury of the University of Utah, Mr. Hugh P. Chrisp of Albany, New York, made some of the drawings used.

Although the collections mentioned above include large series of a number of forms, others are known only from one or a few specimens. Further information concerning the skeletal anatomy of many forms is highly desirable. The osteological notes presented in this paper are based on only the following forms: *graminea, deppii, liocephalus, coerulea, multicarinata, viridiflava, gadovii,* and *imbricata.* A few characters, such as the presence or absence of pterygoid teeth, which could be determined without damage to preserved specimens, were noted in at least one example of every form in which several specimens were available.

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1 Drawn from material submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy from the University of Rochester.

There is much confusion in the literature as to the names applied to certain of the cephalic scutes. This confusion is due in part to a purely arbitrary choice by different authors of different names for the same element, and in part to a lack of recognition of the homologies between different groups of Gerrhonotinae. Figure 1 shows, somewhat diagrammatically, the hypothetical arrangement in a "gerrhonotine prototype." The labeling indicates the names here applied to the various elements; the terminology used is, with minor exceptions, that employed by Smith (1946).

The labels accompanying this figure are, for the most part, self-explanatory, but a few additional remarks will be useful. The median postrostral found in many forms is probably derived from a fusion of the two median anterior internasal elements. The anterior canthal is often fused with the posterior internasal; the term posterior internasal is used to designate this

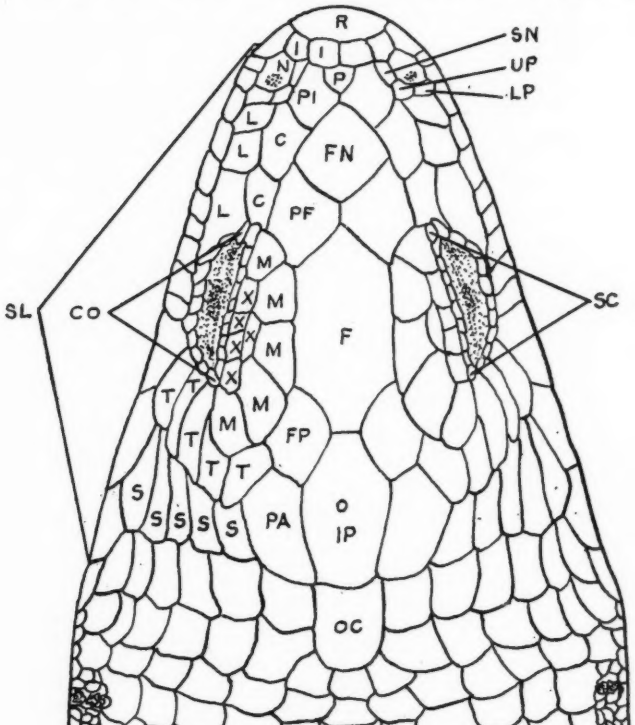


Fig. 1.—Hypothetical arrangement of cephalic scutes in a "gerrhonotine prototype."

compound element as well as the simple posterior internasal. The "posterior loreal" of many forms is of somewhat uncertain origin, perhaps consisting of only the posterior loreal of this hypothetical form, perhaps also including the middle loreal. When the posterior canthal is obviously fused with the posterior loreal, the term "cantholoreal" may be employed, but if there is a question as to whether or not such fusion has occurred, the element is called simply the posterior loreal. In most cases the scales surrounding the eye are well differentiated into preocular, subocular and postocular series.

On the ventral surface of the head, the median anterior element is termed the mental; the scales bordering the mouth opening below are the infralabials. Posterior to the mental are several rather large plates; the most anterior of these, which may be paired or unpaired, is called the postmental, those which follow it the chin shields. A row of rather small elements between the infralabials and the chin shields are termed the sublabials. The posterior limits of these subcephalic scale groups are often difficult to determine, as they tend to grade into the ordinary gular scales.

The number of transverse dorsal scale rows is counted longitudinally beginning with the first row behind the occipital to the posterior border of the thigh; transverse ventral rows are counted along the mid-ventral line from the first chin shields to the preanals, exclusive. Longitudinal dorsal and ventral rows are counted transversely at mid-body, except when otherwise stated.

TAXONOMIC HISTORY

The genus *Gerrhonotus* was proposed by Wiegmann (1828) to include the species *deppii, taeniatus, coeruleus, rudicollis, imbricatus* and *liocephalus,* all described for the first time.

In 1830 Peale and Green described a specimen of *G. liocephalus* under the name of *"Scincus ventralis."* In the text of their article the following statement appears: "We have preferred to consider this animal for the present as a scink, but we are aware, that with a less violation of the arrangements of nature, than that which often occurs on this subject, that we might constitute with it a new genus, under the name of *Ptero-gastenes . . ."* This name of Peale and Green was correctly assigned to the synonymy of *"G. tessellatus"* by Wiegmann in his 1834 *Herpetologia Mexicana, tessellatus* being a name substituted for *liocephalus.*

The first attempt to split Wiegmann's genus was that of Gray in 1838. He recognized four genera: *Abronia,* including *deppii* and *taeniatus*; *Gerrhonotus,* including *coeruleus, tessellatus* and *burnettii*; *Barisia,* including *rudicollis, imbricatus* and *lichenigerus;* and *Elgaria,* including *kingii* and *multicarinata.* These same genera were used by Gray in his 1845 *Catalogue,* although he there changed the spelling of *Barisia* to *Barissia.* This emended spelling is the one that has been used by all subsequent authors. In this same work the name *Ptero-gastenes* Peale and Green erroneously appeared as *Pterogasterus*; this error has likewise been perpetuated.

Fitzinger, in 1843, designated *tessellatus* as the type species of *Gerrhonotus.*

In the same work he proposed four other generic names in this group which have been completely ignored by all subsequent herpetological authors. Those genera were: *Tropidogerrhonotus* (type species *rudicollis*), *Trachypeltis* (type species *multicarinatus*), *Aspidosoma* (type species *taeniatus*) and *Leiogerrhonotus* (type species *deppii*). Actually in his text the names *Tropidogerrhonotus* and *Leiogerrhonotus* appeared in the abbreviated forms of *Tropidogerrhon.* and *Leiogerrhon.* respectively.

I believe there can be little doubt that these are abbreviations rather than complete names, particularly since the name *Gerrhonotus* is at one point abbreviated to *Gerrhon.* Nevertheless, Agassiz's 1846 *Index Universalis* contains, as generic names, these abbreviated forms; they were slightly emended by him, *Leiogerrhon.* becoming *Liogerrhon* and *Tropidogerrhon.* becoming *Tropidogerrhum.* The abbreviated forms and their emendations have appeared in all subsequent works of the same nature. Although in their first appearance these emendations were not accompanied by any description nor by any designation of a genotype, the bibliographic reference to such designation is clear. They are therefore to be considered as strict synonyms of Fitzinger's names, rather than as *nomina nuda.*

Some of Gray's genera were recognized by certain subsequent authors, not by others. There was no further attempt at a clear definition of the gerrhonotine genera until Cope in 1877 proposed to recognize four such genera, *Pterogasterus, Gerrhonotus, Barissia* and *Mesaspis,* the latter then proposed for the first time and containing two forms, *moreleti* and *fulvus.* These genera were defined on the basis of the arrangement of the "prefrontal" and "internasal" elements, features that have since been shown to be extremely variable within certain species. It is also obvious that he was not aware of the proper homologies of certain of these plates among the different groups. Since the characters he used are not at all consistent, there has been a strong tendency to drop these genera. *Barissia* was commonly recognized until recent years, but most writers at present place all of the Gerrhonotinae in the single genus *Gerrhonotus.*

Besides these attempts to split the group into several genera, there have been several attempts to split the large genus *Gerrhonotus* into several "species groups." Most of these arrangements met with the same difficulties as the various generic arrangements. A notable exception, which expresses the natural relationships very closely, is that of Smith (1942).

It is certainly true that the characters used by Gray and by Cope to define their several genera do not, for the most part, possess the significance attributed them by those workers. Nevertheless there are several readily recognizable groups of related forms within the Gerrhonotinae that I believe to be worthy of generic status. For most of these, Gray's names are available, though a complete redefinition of the genera to which they are applied is required. In the present work I propose to recognize five genera, as follows: *Gerrhonotus* Wiegmann, 1828; *Abronia, Elgaria* and *Barisia,* all of Gray, 1838; and a fifth, which is here proposed to contain the single form *rhombifer* from Panama.

The generic concept is open to some differences of opinion; generic rank seems to be in part a matter of actual degree of relationship, and in part a matter of convenience to the taxonomist. Neither of these factors can be ignored entirely in determining whether a particular group should be granted generic status. In the present case the groups recognized as genera are as distantly related as most genera recognized in many other families. These gerrhonotine genera are perhaps not as convenient as some, in the sense that many of the most important generic characters are osteological or comparative, hence not immediately recognizable on casual examination. But they are convenient in that they indicate the relationship among the Gerrhonotinae much more clearly and accurately than would any attempt to recognize only a number of species groups within a single, large, extremely heterogenous genus.

Coloptychon gen. nov.

Genotype.—*Gerrhonotus rhombifer* Peters, 1877 [=*Coloptychon rhombifer* (Peters)].
Range.—Known only from Chiriquí, Panamá.

Definition.[1]—Lateral fold weakly developed, with a very small granular area or none at all; sides of the neck nearly agranular; minimum number of scales across the nape ten or more; anterior internasals present; two azygous postrostrals; circumocular series not differentiated into preocular, subocular and postocular series; ten ventral scale rows.

Discussion.—This genus is known only from a single, probably young, specimen, the type of *rhombifer*, and I have not seen this specimen. I am well aware of the undesirability of proposing a new generic name under such conditions, but fairly adequate descriptions of the specimen are given by Peters and by Bocourt, and excellent figures are furnished by the latter. As judged from these descriptions and figures, there is very little possibility that this species can be assigned to any of the genera of Gerrhonotinae here recognized. It has been suggested to me that this is possibly a teiid rather than an anguid lizard. After comparison with teiids, I consider this very doubtful, since the arrangement of the head plates as shown by Bocourt, though differing in detail from any other known gerrhonotine lizard, is still, in general, gerrhonotine in character, and does not particularly resemble any of the Teiidae. Even though a number of features must for the present remain uncertain, a brief discussion of those that can be determined will show the impossibility of assigning this form to any of the other recognized genera.

The very weak lateral fold and nearly agranular condition of the side of the neck distinguish this form from all other genera excepting *Abronia*. Even in those species of *Abronia* in which the side of the neck is agranular, the scales of that region are modified and differ decidedly from the dorsal scale rows, resembling rather a continuation of the ventral scales. But Bocourt's figure of *rhombifer* shows that, except for a small area just behind the ear, the scales of the side of the neck are perfectly continuous with those of the dorsum.

Although this form slightly resembles *Abronia* in the weak condition of the

1 Osteology unknown.

lateral fold, there are so many striking dissimilarities that the two could not be considered a single genus. *Abronia* never has an azygous postrostral; *rhombifer* has two. *Abronia* never has more than six scales in a single row across the nape; *rhombifer* has at least ten. *Abronia* never has less than twelve ventral scale rows; *rhombifer* has ten. *Abronia* shows a very consistent arrangement of the scales of the loreal region, quite different from that in *rhombifer*. This list could be further extended.

Coloptychon is distinguished from the entire *Gerrhonotus-Elgaria-Barisia* complex by the extremely weak development of the lateral fold, by the possession of two azygous postrostrals, by the lack of differentiation of subocular and postocular groups in the circumocular series, and by the presence of five lateral supraoculars. It is almost perfectly characterized by the possession of only ten ventral scale rows; in rare specimens of *Barisia gadovii* there are a few transverse ventral rows with only ten or eleven scales, and in one example seen it is true of most of the ventral rows. In no other form is the number below twelve in any row near the middle of the body. In addition to these characters in which *Coloptychon* differs from all three of these genera, there are others in which it differs from one or another, but not all.

In view of the above statements, there is no possibility of assigning *rhombifer* to any of the other genera of Gerrhonotinae. Although there is no visible basis for such an assumption, there is always the possibility that the descriptions and figures are erroneous or misleading in certain respects, and that actual examination of the specimen would not support the conclusion drawn. It might therefore seem desirable to refer *rhombifer* to some such category as "incertae sedis"; such a procedure, however, appears to me inadequate. The purpose of any taxonomic review is not only to present the evidence bearing on the problems concerned, but also to offer the interpretation of such evidence which seems to the writer most reasonable and logical; a category such as "incertae sedis" often serves to avoid this responsibility.

The present genus, *Coloptychon*, is the most primitive of all the living Gerrhonotinae; in it are found practically none of the specializations and modifications that are described in other genera. A comparison of Bocourt's figures of *rhombifer* (reproduced here as Figures 2 and 3) with the diagram of the hypothetical gerrhonotine prototype shows a strong degree of similarity. There are, of course, several differences, but these are fewer in number and for the most part less important than the differences btween the theoretical form and other gerrhonotine genera.

Since only one species is known, it will be described here in some detail.

COLOPTYCHON RHOMBIFER (Peters)

Gerrhonotus rhombifer Peters, 1877, Monatsber. k. Pr. Akad. Wiss. Berlin, 1876: 298.

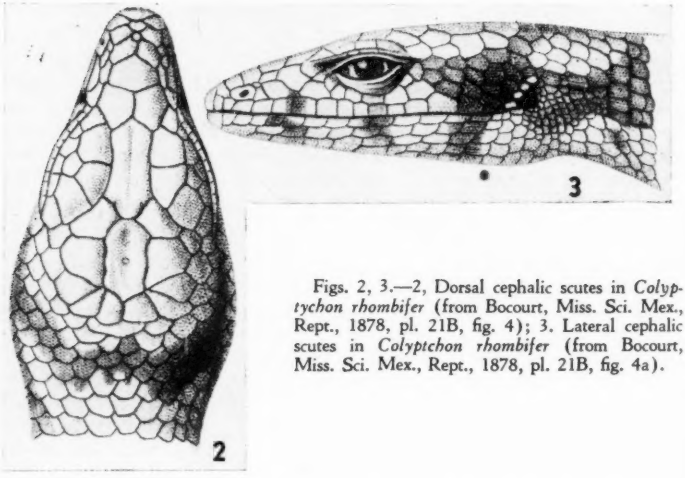
Gerrhonotus (*Abronia*) *rhombifer*, Bocourt, 1878, Miss. Sci. Mex., Rept., livr. 5: 332, pl. 218, figs. 4, 4a.

Type and type locality.—Berlin Museum 8655. A presumably young specimen from Chiriquí, Panamá.

Range.—Known only from the type locality.

Diagnosis.—Essential specific characters the same as those of the genus.

Description.—Nasal separated from the rostral by the anterior internasals. Two azygous postrostrals, in contact with each other, the anterior between the anterior internasals and expanded supranasals, the posterior between the expanded supranasals and the posterior internasals. Frontonasal present, in contact with the anterior canthal, separated from the frontal by the prefrontals. Two superposed postnasals. Three loreals, the second not reaching the



Figs. 2, 3.—2, Dorsal cephalic scutes in *Colyptychon rhombifer* (from Bocourt, Miss. Sci. Mex., Rept., 1878, pl. 21B, fig. 4); 3. Lateral cephalic scutes in *Colyptchon rhombifer* (from Bocourt, Miss. Sci. Mex., Rept., 1878, pl. 21B, fig. 4a).

labials, and an anterior canthal present. Five medial and five lateral supraoculars, four of the latter in contact with the superciliaries, the fifth interposed between those and the medial row. Frontal in contact with the large interparietal, which is in contact with a paired interoccipital. There appear to be about nine superciliaries, the anterior small, not in contact with the prefrontals. About nine circumocular elements, not differentiated into pre-, sub- and postocular series. Five primary and five (?) secondary temporals, the uppermost primary in contact with the uppermost secondary and the lowest primary in contact with only the lowest secondary. Fourteen supralabials; eleven or twelve infralabials.

Dorsals in sixteen to eighteen and ventrals in ten longitudinal series; number of transverse rows uncertain. Dorsal scales quite smooth, so the dorsal osteoderms are presumed to be thin and smooth; this is probably a juvenile characteristic. Number of caudal whorls unknown. The scales of the side of the neck are perfectly continuous with those of the dorsum except for a small area just behind the ear. Lateral fold very weak.

Color description from Boulenger's *Catalogue*: "Upper surface of the head and eight irregular rhomboidal spots on the body, yellowish-white, separated

by narrow dark brown interspaces; tail annulate brown and yellowish; belly blackish."

The measurements of the type as given by Peters and by Bocourt are:

	Peters	Bocourt
Total length	150 mm.	145 mm.
Head	12 mm.	12 mm.
Width of head	—	7 mm.
Snout to anus	—	49 mm.
Fore limb	11 mm.	11 mm.
Hind limb	14 mm.	13 mm.
Tail	100 mm.	96 mm.

Relationships.—This is the only known form of the genus. The only other gerrhonotine lizard known to occur in this area is *Barisia monticola*, with which *C. rhombifer* could scarcely be confused.

ABRONIA Gray

Abronia Gray, 1838, Ann. Mag. Nat. Hist., ser. 1, 1: 389.
Aspidosoma Fitzinger, 1843, Syst. Rept.: 21.
Leiogerrhonotus Fitzinger, 1843, Syst. Rept.: 21.
Liogerrhon Agassiz, 1846, Nomencl. Zool. Ind. Univ.: 203.

Genotype.—*Gerrhonotus deppii* Wiegmann, 1828 [=*Abronia deppii* (Wiegmann)]. By present designation.

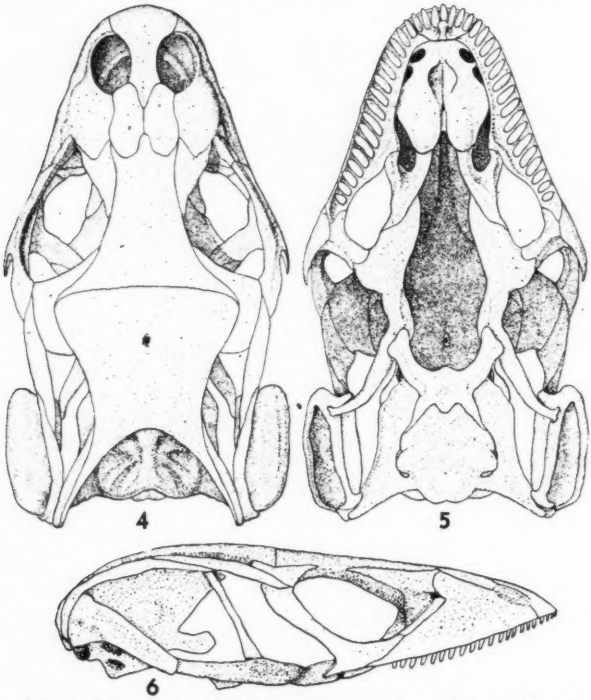
Range.—From Guatemala northward to southern Guerrero and southern Hidalgo.

Definition.—Gerrhonotine lizards with the skull widened and depressed; frontal bones narrowly separated from the maxillae; pterygoid teeth absent; dorsal osteoderms without a well-defined, strongly thickened basal area; lateral fold weakly developed, containing few or no true granules; sides of the neck coarsely granular to agranular; ventrals in twelve to fourteen rows; minimum number of scales in a single row across the nape four to six; anterior internasals present; no postrostral; subocular and postocular series well differentiated from each other; the suboculars usually do not reach the lowest primary temporal.

Discussion.—This genus is the best defined and most easily recognizable of any of the gerrhonotine genera proposed by Gray, but it is the only one of those genera that has never been granted recognition by any subsequent author. Bocourt recognized this group as constituting a subgenus of *Gerrhonotus*, including in it all the then known species here referred to the genus, and also *C. rhombifer*. Other authors have recognized this same assemblage as a group of species, but no one since Gray has granted it full generic rank.

The widening and flattening of the skull is quite evident on superficial examination, as may be seen by comparisons of drawings of the skull (Figs. 4-6) with those of other gerrhonotine skulls. The statement as given in the generic definition may seem to imply that this is a subjective character, but actually a variety of objective proportional measurements demonstrate this feature. Of these, the most useful is the fact that the pterygoids are widely separated; their distance from each other at the level of the basipterygoid process is well over half of the distance from that point to the posterior end of the pterygopalatine suture, as compared with less than half — usually much

less — in other genera of the group. This character can be determined without damage to a preserved specimen other than removal of the mucous lining from the roof of the mouth. The length of the frontoparietal suture is greater than the greatest depth of the head in *Abronia,* less in other genera. The



Figs. 4-6.—4. Dorsal view of skull of *Abronia graminea,* ×3½; 5. Ventral view of skull of *Abronia graminea,* ×3½; 6. Lateral view of skull of *Abronia graminea,* ×3½. Figs. 4, 5 drawn by Hugh P. Chrisp.

depth of the head at the posterior end of the parietal (excepting the arches) is, in *Abronia,* slightly over half the distance between the posterior ends of the maxillae, in other genera about two-thirds of that distance.

Several other osteological features distinguish this genus from certain of the other genera, but are not confined to *Abronia.* The occipital and otic elements are fused into a single compound bone. The nasals are in contact with each other along the mid-dorsal line, between the frontal and the premaxilla. The frontal is narrowly separated from the maxillae by a contact of the prefrontal with the nasal on each side. Pterygoid teeth are completely lacking.

The dorsal osteoderms are typically very heavy and rugose, somewhat

thicker in their mid-portion than along their sides, but lacking a definite keel. In some forms the basal portion (*i.e.*, the region overlapped by the next anterior osteoderm) is in no way distinguishable from the remainder; in others this basal portion may be somewhat smoother than the remainder, but is not strongly thickened as in other genera. In a number of forms there is a tendency towards reduction of the dorsal osteoderms; they become very thin and relatively smooth. In one species (*deppii*) they have disappeared completely over most of the body.

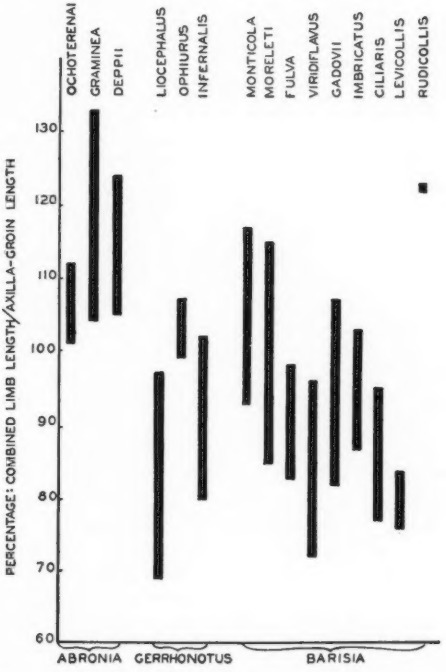


Fig. 7.—Ranges of variation in relative limb lengths of various genera and species of gerrhonotine lizards.

The lateral fold is most weakly developed in *deppii*. It contains no granules but only small, mostly overlapping scales. The side of the neck in that form is likewise devoid of true granules. Some members of the genus have the side of the neck granular, but the granules are coarse in comparison with those found in other genera. In some the lateral fold contains a granular area which is very narrow, not equal in width to one of the lateral scale rows. The degree of granulation of the postero-ventral surfaces of the shank and forearm is somewhat variable.

So far as is known, the members of this genus are arboreal, in contrast to the others, which are almost exclusively terrestrial. The predominance of greens and, in a few cases, gray-browns in the color patterns of this group is probably a reflection of this habit. The limbs and the digits are relatively longer and stronger in *Abronia* than in other genera (cf. Figure 7); this also is probably correlated with the arboreal habits.

Certain characteristics of scalation are common to all members of the genus. Anterior internasals are always present; sometimes two elements are present on one or both sides, but in no case is the arrangement such that any of these elements would be considered a postrostral. The nasal is never in contact with the rostral. There are normally two small superposed postnasals; in most forms a supranasal is also present. An anterior loreal and a posterior cantholoreal are always present; the anterior canthal may or may not be present as an independent element. The number of lateral supraoculars is usually three; two or four occur occasionally. The superciliary series comprises a variable number of elements and is normally complete. The subocular and postocular series are well differentiated from each other; the former in most cases does not extend to the lowest primary temporal, but such a condition obtains in a few specimens of *graminea*. Frontonasal present or absent.

The scales of the body, particularly the dorsals, are relatively large, and the number of transverse dorsal rows quite low. Only in *matudai*, and perhaps rarely in *taeniata*, are there more than thirty-five transverse rows of dorsals; with the exception of two species of *Barisia* the number of transverse rows of dorsals always exceeds forty in other genera. In most species of *Abronia* the minimum number of scales counted transversely in any one row across the nape is six; this number may be lower, but is never higher. The number of transverse rows of ventrals and the number of caudal whorls are likewise, in general, lower in *Abronia* than in other genera, but the difference is not so striking as in the case of the dorsals.

This genus seems to have been an early branch of the gerrhonotine stock, not particularly closely related to any of the other living genera. It retains certain primitive characters not found elsewhere, but it is also in some respects the most highly modified of the group. The osteoderms, in those forms in which they are well developed, are of a type strongly resembling that found in *Peltosaurus* and other fossil anguid genera; this type is therefore thought to be primitive. The weak condition of the lateral fold is likewise regarded as primitive, rather than degenerate. On the other hand, *Abronia* shows a moderate degree of specialization in reduction of the number of head scales, and a greater degree in reduction of the number of body scales. The absence of pterygoid teeth and, above all, the shape of the skull, are considered to be rather highly specialized features. This genus, then, while probably one of the earliest branches of the gerrhonotine line, cannot be considered as any more primitive, or, in other words, any more similar to the ancestral stock, than can the other living genera.

Ten known forms are recognized in this genus. These are:

Abronia deppii (Wiegmann), 1828. Isis, 3: 379-380 (type locality "Mexico").
Abronia taeniata taeniata (Wiegmann), 1828. Isis, 3: 380-381 (type locality "Mexico").

Abronia taeniata graminea (Cope), 1864. Proc. Acad. Nat. Sci. Philadelphia, 16: 179 type locality Orizaba, Veracruz, Mexico).
Abronia fuscolabialis (Tihen), 1944. Copeia, 1944: 112-115, figs. 1-3 (type locality Mt. Zempoaltepec, Oaxaca, Mexico).
Abronia oaxacae (Günther), 1885. Biologia Centrali-Americana, Rept. Batr.: 36, pl. 24, fig. A (type locality "Oaxaca," Mexico).
Abronia aurita (Cope), 1868. Proc. Acad. Nat. Sci. Philadelphia, 20: 306 (type locality "Verapaz," Guatemala).
Abronia fimbriata (Cope), 1885. Proc. Amer. Philos. Soc., 22: 171 (type locality Alta Verapaz, Guatemala).
Abronia ochoterenai (Martín del Campo), 1939. Anal. Inst. Biología (Mexico), 10: 357-359, fig. 3 (type locality Santa Rosa, Comitán, Chiapas, Mexico).
Abronia matudai (Hartweg and Tihen), 1946. Occas. Papers Mus. Zool. Univ. Mich., 497: 3-5 (type locality 2000 m., Volcán Tacaná, Chiapas, Mexico).
Abronia vasconcelosii (Bocourt), 1872. Nouv. Arch. Mus. Hist. Nat. Paris, 7: 107 (type locality Argueta, Guatemala).

GERRHONOTUS Wiegmann

Gerrhonotus Wiegmann, 1828, Isis, 1828, no. 3: 379.
Ptero-gastenes Peale and Green, 1830, Journ. Acad. Sci. Philad., 6: 234.
Pterogasterus Gray, 1845, Cat. Spec. Liz. Coll. Br. Mus.: 53.

Genotype.—*Gerrhonotus tessellatus* Wiegmann, 1834 [= *Gerrhonotus liocephalus* Wiegmann, 1828]. By designation of Fitzinger, 1843.

Range.—Southwestern Chiapas northward to southern and central Texas.

Definition.—Gerrhonotine lizards with the skull not widened or depressed; frontal in contact with the maxillae; pterygoid teeth present, well developed; dorsal osteoderms with a well-defined, strongly thickened basal area; lateral fold strongly developed, with a broad granular area; sides of the neck finely granular; shank and forearm agranular or nearly so; minimum number of scales in any one row across the nape eight to ten; anterior internasals present; postrostral present; subocular and postocular series well differentiated from each other; the suboculars not extending to the lowest primary temporal; twelve to fourteen ventral scale rows.

Discussion.—The matter of skull shape has been rather thoroughly treated in connection with *Abronia,* and that discussion need not be repeated. In this respect *Gerrhonotus, Elgaria* and *Barisia* are in very close agreement.

The exoccipitals and otic elements are fused into a single bone on each side, but the basi- and supraoccipital are independent. The nasals are in contact with each other along the mid-dorsal line between the frontal and the premaxilla. The frontal is in contact with the maxillae between the prefrontals and nasals. Pterygoid teeth are present, numerous, well developed.

The dorsal osteoderms are moderately heavy and only slightly rugose. They possess a well defined, greatly thickened basal area and a strong, rather acute median keel.

The lateral fold is strongly developed, containing a granular area equivalent to about two lateral scale rows in width; the side of the neck is finely granular. There is a small but deep and well defined axillary dermal pocket, usually also a less well defined postfemoral pocket. The posteroventral surfaces of the thighs and upper arms are granular or subgranular, but the shank and forearms are without granules, or at most with one row which might be

considered granular. A similar condition occurs in *Elgaria,* but in *Barisia* the shank and forearm both contain several rows of definite granules.

Members of this genus are large, elongate lizards with rather well developed limbs. Head proportions and limb proportions are similar to those found in *Barisia* and *Elgaria.* The tail is very long, 1¾ to about 2½ times the snout-vent length, this ratio varying markedly from one form to another. Although there is some overlap in this ratio between *G. l. infernalis* (with the lowest such ratio found in the genus) and a few forms of *Barisia,* in no case is the average tail/body ratio in any form of *Barisia* as high as the average for *infernalis.* Several forms in the genus *Elgaria* have tail/body ratios comparable to the shorter-tailed forms of *Gerrhonotus.*

These are terrestrial lizards, as are the members of *Elgaria* and *Barisia.* The basic dorsal color is brown, nearly uniform or with darker transverse bands, which usually contain white-tipped scales. There is no tendency toward a broad dorsal longitudinal band of the type found in most species of *Barisia* and in some *Elgaria.*

Members of this genus are liberally provided with scales, both on the head and on the body, being surpassed only by *Coloptychon* in this respect. Anterior internasals are always present, separating the nasal from the rostral; there is a single postrostral; frontonasal always present. There are at least two loreals and one (anterior) canthal, frequently more. The number of supralabials (rarely as low as ten, up to fourteen) and infralabials (nine to thirteen) is high as compared with other genera. The superciliary series is complete, always comprising at least five elements. The postmental is always paired and is followed by four large and one or two smaller chin shields, as compared with usually three large and one smaller shields in other genera. There are usually sixteen longitudinal and at least forty-five transverse rows of dorsals, usually over sixty transverse rows of ventrals, and over 115 caudal whorls.

The large size, elongate body and tail, well developed lateral fold, and perhaps the color pattern, are regarded as specialized characters, but in all other respects mentioned above this genus is considered primitive. Concise definition of the genus is thus made more difficult, since specialization in the groups of *Elgaria* and *Barisia* has proceeded along different lines, with different primitive characters retained in each. Therefore, in one form or another of these genera most of the primitive characteristics of the genus *Gerrhonotus* can be found, but when *Gerrhonotus* is regarded as an assemblage of such primitive characteristics, it is obvious that no single form or group in the other two genera resemble it closely. A few *Barisia,* such as *B. gadovii,* have retained, at least as a variant, a type of cephalic scutellation very similar to that of *G. l. liocephalus,* but these differ widely from *Gerrhonotus* in color pattern and, as do all *Barisia,* in degree of granulation of the limbs and in skull structure. Some *Elgaria,* such as *multicarinata,* resemble *Gerrhonotus* in proportions, in general color pattern, and in certain osteological respects, but these and all other *Elgaria* show important specializations in cephalic scutellation never found in *Gerrhonotus,* as well as minor differences in skull structure. Only one seemingly minor character of scalation has been noted which will serve almost perfectly to distinguish *Gerrhonotus* from all members

of both *Barisia* and *Elgaria*; this is the fact that in the former the subocular series does not extend to the primary temporal series, while in the latter two it is normally in contact with the lowest member of that series. Osteologically *Gerrhonotus* is distinguished from the other two genera by the maxillary-frontal contact. Other characters mentioned in the generic definition serve to separate this genus from either *Elgaria* or *Barisia*, but not from both.

As the foregoing discussion indicates, *Elgaria*, *Barisia* and *Gerrhonotus* are more closely related to each other than are any of these to *Abronia* or *Coloptychon*, and of the three, *Gerrhonotus* is regarded as having retained more of the characteristics of their common ancestor than has either of the others. The northern representatives of the genus are thought to be only slightly modified from the early common stock of the three genera, at least in respect to scalation. There are a few features, already mentioned, which must be considered as subsequent modifications acquired by this genus.

Five known forms are recognized in this genus:

Gerrhonotus liocephalus liocephalus Wiegmann, 1828. Isis, 3: 381 (type locality "Mexico").

Gerrhonotus liocephalus austrinus Hartweg and Tihen, 1946. Occas. Papers Mus. Zool. Univ. Mich., 497: 6-7 (type locality Cerro Malé, Porvenir, Chiapas, Mexico).

Gerrhonotus liocephalus infernalis Baird, 1858. Proc. Acad. Nat. Sci. Philadelphia, 10: 255 (type locality Devils River, Texas).

Gerrhonotus liocephalus loweryi Tihen, 1948. Trans. Kans. Acad. Sci., 51 (3): 302 (type locality the Xilitla region, San Luis Potosí, Mexico).

Gerrhonotus liocephalus ophiurus Cope, 1866. Proc. Acad. Nat. Sci. Philadelphia, 18: 321 (type locality Orizaba, Veracruz, Mexico).

ELGARIA Gray

Elgaria Gray, 1838, Ann. Mag. Nat. Hist., ser. 1, 1: 390.
Trachypeltis Fitzinger, 1843, Syst. Rept.: 21.

Genotype.—*Cordylus* (*Gerrhonotus*) *multicarinatus* Blainville, 1835 [=*Elgaria multicarinata multicarinata* (Blainville)]. By present designation.

Range.—Chihuahua and Baja California northward to southern British Columbia.

Definition.—Gerrhonotine lizards with the skull not widened or depressed; frontal not in contact with the maxillae; pterygoid teeth present, well developed; dorsal osteoderms with a well-defined, strongly thickened basal portion; lateral fold well developed, with a large granular area; sides of the neck finely granular; shank and forearm agranular or nearly so; minimum number of scales in a single row across the nape eight to ten; twelve ventral scale rows; anterior internasals lacking; postrostral normally absent; subocular and postocular series well differentiated from each other; suboculars extending to the lowest primary temporal.

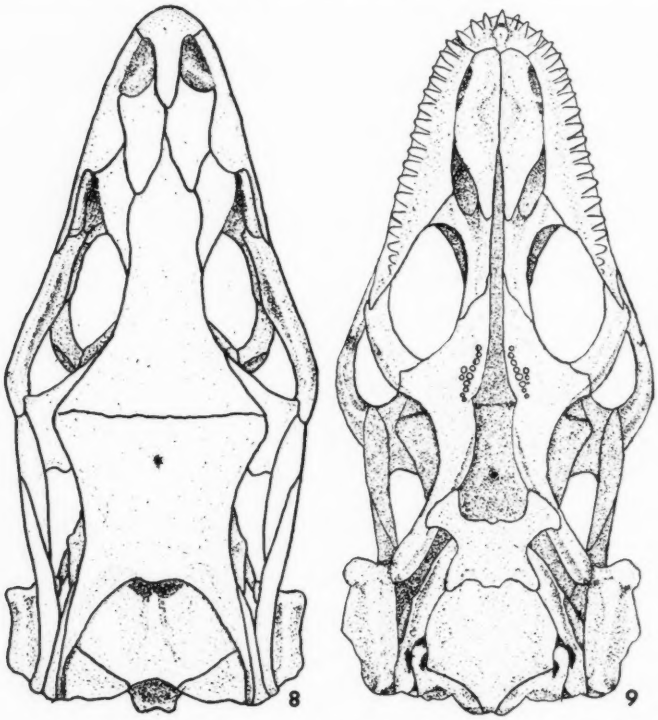
Discussion.—Skull proportions are essentially the same as in *Gerrhonotus* and *Barisia*. The exoccipitals and otic elements are fused into a single bone on either side but the basi- and supraoccipital are independent. The nasal bones are in contact with each other along the mid-dorsal line between the frontal and the premaxilla. The frontal is separated from the maxillae by a contact of the prefrontals with the nasals. Pterygoid teeth are present, numerous and well developed.

The dorsal osteoderms are moderately heavy to thin, only slightly rugose or quite smooth. They possess a well-defined, strongly thickened basal area, and usually a strong, rather acute median keel, although the latter is greatly reduced or lacking in certain forms.

The lateral fold is strongly developed, containing a granular area more than equivalent to one lateral scale row in width; the side of the neck is finely granular. There is no well-defined gular, axillary, or post-femoral dermal pocket. The posteroventral surfaces of the thighs and upper arms are granular, of the shanks and forearms agranular or nearly so.

Members of this genus are of moderate to large size, none being as small as certain members of the genus *Barisia* and only a few as large as the larger members of that genus, or as the members of *Gerrhonotus*. The tail is variable in length, relatively short in *coerulea* but comparable to *Gerrhonotus* in *multicarinata* and related forms.

Like the preceding, this genus comprises only terrestrial forms. Some



Figs. 8-9.—8. Dorsal view of skull of *Elgaria c. coerulea;* 9. Ventral view of skull of *Elgaria c. coerulea.*

members of *Elgaria* occur at lower altitudes than are recorded for representatives of any of the other gerrhonotine genera. The basic dorsal color is usually brown, occasionally grayish. In *coerulea* there is a tendency towards possession of a mid-dorsal longitudinal band, but in other species the pattern consists primarily of dark brown transverse bands on a lighter ground color; even in *coerulea* transverse bands frequently occur.

An outstanding feature of the scalation of *Elgaria* is the universal absence of the anterior internasals, the expanded supranasals forming the first pair of scales behind the rostral, the nasals in contact with the rostral lateral to the supranasals. The frontonasal is always present. With the exception of a single anomalous specimen seen, the postrostral is always lacking. The loreocanthal region is somewhat variable, but typically contains an anterior loreal, an anterior canthal and a posterior cantholoreal. Usually there are two superposed postnasals, but this character is subject to some variation. The superciliary series is complete, usually comprising five elements. The postmental is always paired, and is followed by three large and one or two smaller chin shields on each side. The number of transverse dorsal scale rows is, in general, high, but varies from forty to sixty. The number of transverse ventral rows is correspondingly rather high in most forms.

This genus is in many respects similar to *Gerrhonotus*. The most prominent difference is the absence of anterior internasals and the postrostral in *Elgaria*. As previously stated, the suboculars always extend to the lowest primary temporal in *Elgaria*, never in *Gerrhonotus*. Osteologically this genus is distinguished by the prefronto-nasal contact, resembling *Barisia* rather than *Gerrhonotus* in that feature.

Thirteen known forms are recognized in this genus:

Elgaria coerulea coerulea (Wiegmann), 1828. Isis, 21: 380 (type locality San Francisco, California).

Elgaria coerulea principis Baird and Girard, 1852. Proc. Acad. Nat. Sci. Philadelphia, 6: 17 (type locality Oregon and Puget Sound).

Elgaria coerulea shastensis (Fitch), 1934. Copeia, 1934, : 6 (type locality South side of Burney Creek, 3000 ft., 2 miles southwest of Burney, Shasta Co., California).

Elgaria coerulea palmeri (Stejneger), 1893. N. Amer. Fauna, 7: 196 (type locality South Fork of Kings River, Fresno Co., California).

Elgaria utahensis (Woodbury), 1945. Proc. Biol. Soc. Washington, 58: 6-8, pls. 1-2 (type locality Sink Valley, south of Alton, 20 miles north of Kanab, Kane Co., Utah).

Elgaria paucicarinata (Fitch), 1934. Copeia 1934: 173 (type locality Todos Santos, Baja California).

Elgaria cedrosensis (Fitch), 1934. Copeia 1934: 6 (type locality Cedros Island, Baja California).

Elgaria multicarinata multicarinata (Blainville), 1835. Nouv. Ann. Mus. Hist. Nat., 4: 57 (type locality California).

Elgaria multicarinata scincicauda (Skilton), 1849. Amer. Journ. Sci. Arts (2), 7: 202 (type locality The Dalles, Wasco Co., Oregon).

Elgaria multicarinata webbii (Baird), 1858. Proc. Acad. Nat. Sci. Philadelphia, 10: 255 (type locality "San Diego to El Paso," restricted to San Diego, San Diego Co., California).

Elgaria multicarinata nana (Fitch), 1934. Copeia 1934: 7 (type locality South Island, Los Coronados Islands, Baja California).

Elgaria kingii kingii Gray, 1838. Ann. Mag. Nat. Hist., 1: 390 (type locality "Mexico").

Elgaria kingii nobilis Baird and Girard, 1852. Proc. Acad. Nat. Sci. Philadelphia, 6: 129 (type locality Fort Webster, New Mexico).

BARISIA Gray

Barisia Gray, 1838, Ann. Mag. Nat. Hist., ser. 1, 1: 390.

Tropidogerrhonotus Fitzinger, 1843, Syst. Rept.: 21.

Barissia Gray, 1845, Cat. Spec. Liz. Coll. Br. Mus.: 54.

Tropidogerrhum Agassiz, 1846, Nomencl. Zool., Ind. Univ.: 203.

Mesaspis Cope, 1877, Proc. Amer. Philos. Soc., 17: 96.

Genotype.—*Gerrhonotus imbricatus* Wiegmann, 1828 [= *Barisia imbricata imbricata* (Wiegmann), 1828]. This designation was made by Stejneger (1890) and applied to the variant spelling "*Barissia*," originated by Gray, 1845. This designation is presumably applicable to *Barisia* Gray, 1838, but to avoid any possible complications, I here designate *imbricata* as the type species of the genus *Barisia* Gray, 1838. I also designate *Gerrhonotus moreleti* Bocourt, 1871 = *Barisia moreleti moreleti* (Bocourt) as the type species of the genus *Mesaspis* Cope, 1877.

Range.—Panama northward through Central America and Mexico to Chihuahua and Coahuila.

Definition.—Gerrhonotine lizards with the skull not widened or depressed; frontal not in contact with the maxillae; pterygoid teeth absent or vestigial; dorsal osteoderms with a well-defined, strongly thickened basal area; lateral fold moderately to well developed, with a moderate or large granular area; sides of the neck finely granular; posteroventral surfaces of the forearms and shanks granular; minimum number of scales in a single row across the nape six to ten; anterior internasals present; postrostral present or absent; subocular and postocular series well differentiated from each other; suboculars extending to the lowest primary temporal; twelve to fourteen ventral scale rows.

Discussion.—The general skull form is essentially the same as in the preceding two genera. The exoccipitals and otic elements are fused into a single bone on each side, the basi- and supraoccipital independent. The nasal bones are separated from each other by a fronto-premaxillary contact in most forms, but are in contact with each other between the frontal and premaxilla in some. The frontal is separated from the maxillae to a varying extent by a contact between the nasals and prefrontals. Pterygoid teeth are completely lacking in most forms; in some a few vestigial teeth are usually present, but they are few in number and very poorly developed, seldom protruding through the mucous lining of the roof of the mouth.

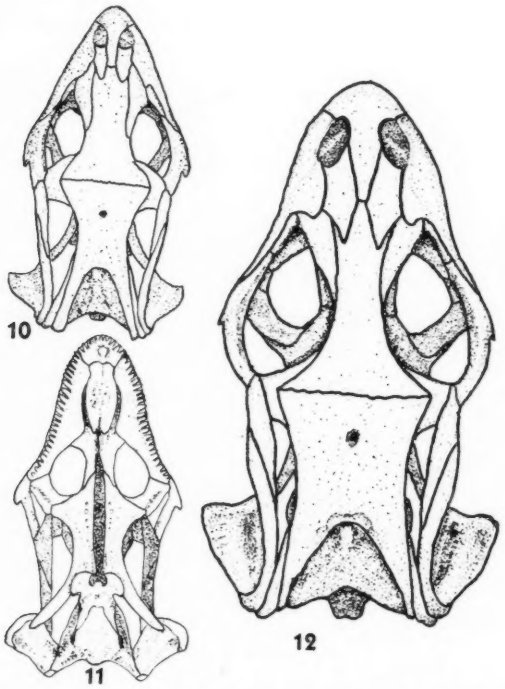
The dorsal osteoderms vary in thickness and are only moderately or slightly rugose. They possess a well-defined, greatly thickened basal area; there is usually a median keel, rather obtuse although sometimes fairly strong.

The lateral fold is moderately to strongly developed, containing a granular

area about equivalent in width to one of the lateral scale rows, or more. The sides of the neck are finely granular, often containing a rather well developed dermal pocket ventromedially. The posteroventral surfaces of the thighs and upper arms are strongly granular, those of the forearms and shanks usually so — always with several rows of definitely granular elements.

The members of this genus are extremely variable in size; it contains the smallest Gerrhonotinae and also some that approach the genus *Gerrhonotus* in size. In general, they have shorter, stouter bodies, less well developed limbs, and a shorter tail than *Gerrhonotus*. The tail is, with few exceptions, less than 1¾ times the snout-vent length.

Barisia, like *Gerrhonotus* and *Elgaria,* is primarily a terrestrial genus. The dorsal color is black to brown, or occasionally olive. There is a strong tendency toward possession of a color pattern in which the elements are primarily longitudinal, in contrast to the predominantly transverse patterns of other genera. A broad mid-dorsal longitudinal band is more or less prominently developed in all forms excepting those few which are nearly uniform in color.



Figs. 10-12.—10. Dorsal view of skull of *Barisia i. imbricata;* 11. Ventral view of skull of *Barisia i. imbricata.* 12. Dorsal view of skull of *Barisia gadovii.*

This is a rather heterogenous genus, apparently containing three major lines of specialization, each with its own peculiar characteristics of scalation. Anterior internasals are always present; the postrostral is present or absent; the frontonasal is present or absent; and the loreocanthal series is extremely variable. The superciliary series may be complete or incomplete; there are one or two postnasals; the postmental is paired or unpaired, followed by a variable number of chin shields. The number of transverse dorsal and ventral rows is quite variable, but is in general somewhat lower than in *Elgaria* and *Gerrhonotus*.

The more important characters distinguishing all members of this genus from either *Gerrhonotus* or *Elgaria* have already been mentioned in connection with these genera.

Fifteen known forms are recognized in this genus:

Barisia moreleti moreleti (Bocourt), 1872. Nouv. Arch. Mus. Hist. Nat. Paris, 7: 102 (type locality Alta Verapaz, Guatemala).

Barisia moreleti fulva (Bocourt), 1872. Nouv. Arch. Mus. Hist. Nat. Paris, 7: 104 (type locality Totonicapam, Guatemala).

Barisia moreleti rafaeli (Hartweg and Tihen), 1946. Occas. Papers Mus. Zool. Univ. Michigan, 497: 8-10 (type locality 16 kilometers south of Siltepec, Chiapas, Mexico, 2300 m.).

Barisia moreleti salvadorensis (Schmidt), 1928. Zool. Ser. Field Mus. Nat. Hist., 12: 196-197, fig. 1 (type locality Esesmiles, Chalatenango, El Salvador).

Barisia moreleti temporalis (Hartweg and Tihen), 1946. Occas. Papers Mus. Zool. Univ. Mich., 497: 10-14 (type locality 2300 m., 11 kilometers southeast of Ciudad de las Casas, Chiapas, Mexico).

Barisia monticola (Cope), 1877. Proc. Amer. Philos. Soc., 17: 97 (type locality Pico Blanco, 11,500 ft., Costa Rica).

Barisia viridiflava (Bocourt), 1873. Ann. Sci. Nat., 17(2): 1 (type locality "Mexico").

Barisia modesta (Cope), 1877. Proc. Amer. Philos. Soc., 17: 97 (type locality "probably Guatemala").

Barisia antauges Cope, 1866. Proc. Acad. Nat. Sci. Philadelphia, 18: 132 (type locality Orizaba, Veracruz, Mexico).

Barisia gadovii (Boulenger), 1913. Ann. Mag. Nat. Hist. (8), 12: 564-565 (type locality Omilteme, Guerrero, Mexico).

Barisia imbricata imbricata (Wiegmann), 1828. Isis, 3: 381 (type locality "Mexico").

Barisia imbricata planifrons (Bocourt), 1879. Miss. Sci. Mex., Rept., livr. 6: 361-363, pl. 21C, fig. 1 (type locality "Oaxaca," Mexico).

Barisia imbricata ciliaris (Smith), 1942. Proc. U. S. Nat. Mus., 92: 365-367 (type locality Sierra Guadalupe, Coahuila, Mexico).

Barisia levicollis Stejneger, 1890. Proc. U. S. Nat. Mus., 13: 184-185 (type locality "Mexican Boundary").

Barisia rudicollis (Wiegmann), 1828. Isis, 3: 380-381 (type locality "Mexico").

GENERAL REMARKS

There are four genera of the Anguidae known from North America as fossils, *Glyptosaurus, Peltosaurus, Melanosaurus* and *Xestops*. The last-named genus is of very uncertain affinities, even as to family; the other three appear more closely associated with the Gerrhonotinae than with any other anguid group in existence at the present time. These three genera share with the Gerrhonotinae the possession of a single parietal bone, differing from all other anguids in this respect. Camp (1923), in distinguishing a family "Glyptosauridae" including these fossil genera, mentioned the strong curvature of the posterior portion of the lower jaw as one of the features of that group; according to Gilmore (1928), "an equal curvature of the posterior portion of the ramus is also to be observed in *Gerrhonotus* [=Gerrhonotinae]." In this fossil group and in the Gerrhonotinae the angular has "an extensive external surface covering the surangular as a thin plate." Those forms of *Peltosaurus* and *Melanosaurus* in which the scutellation of the head is moderately well known exhibit a strong resemblance to the general pattern of scutellation found in the Gerrhonotinae (cf. Gilmore, figs. 76 and 83). In this feature *Glyptosaurus* differs widely from the other genera, both fossil and Recent.

I believe it proper to conclude that the gerrhonotine line was established, or was being established, at the time of the existence of *Peltosaurus* and *Melanosaurus*. Since *Melanosaurus maximus* is known from the Lower Eocene, and undetermined species which Gilmore states "may be safely referred to the genus *Peltosaurus*" occur in the Paleocene, an early origin for the group is indicated.

As is true in several reptile groups, the evidence in the case of the Gerrhonotinae points to the northern Mexican plateau as the center of dispersal. At the present time only the more specialized forms of the group are found in that region; the more peripheral forms exhibit a progressively greater number of primitive features, corresponding closely with their distance from the assumed center of dispersal. In some cases forms at opposite peripheries of the range show a strong resemblance to each other in certain primitive characters not found elsewhere in the group, even though other features in each form may have been so modified that generic separation is warranted. Thus *Abronia* in southern Mexico and northern Central America seems to have its closest counterpart in the fossil *Peltosaurus* of the northwest central United States. The Central American *moreleti* complex of *Barisia* bears a strong resemblance in certain features to *Elgaria coerulea* at the opposite periphery of the range of the group.

The best explanation for these facts is the assumption of a geographically centrally located common ancestor. It appears that major modifications have occurred primarily near the center of the range, the more primitive forms moving outwards from this center. The reverse procedure — progressive specialization occurring as outward emigration proceeded — has in some cases played an important part in the production of lesser systematic groups, but the major changes have occurred near the center of the range.

The gerrhonotine ancestral stock was probably established in the region of the northern Mexican plateau at the very beginning of the Cenozoic Era.

A very early and rapid modification and spread of this group occurred, so that in the Lower Eocene the picture was probably as follows: The population near the center of dispersal represents the *Gerrhonotus-Elgaria-Barisia* ancestral stock, with a moderately strong lateral fold, non-tubercular osteoderms, an essentially unmodified skull, and a type of cephalic scutellation probably similar to that of *Gerrhonotus l. infernalis*. More peripherally are groups that have retained the primitive tubercular osteoderms and the weakly developed lateral fold, but have acquired certain other characteristics not found elsewhere, developing into the *Peltosaurus-Melanosaurus* complex in the north, into *Abronia* in the south. The only place where a form closely resembling the original primitive stock has managed to survive is at the extreme southern periphery of the range — Panama; *Coloptychon* represents a slightly modified remnant of this group. The entire group, even at this early stage, was probably pretty well limited to rather high altitudes. During the remainder of the Eocene little further major change occurred. Partial submergence of the Isthmus of Tehuantepec during the Middle and Upper Eocene may have been a factor in bringing about the present arrangement of species of Abronia. Also, the inundation of southern Nicaragua during the Upper Eocene must have effectively isolated the *Coloptychon* prototype from the more centrally located members of the group.

Another period of rapid modification in and emigration from this northern plateau region is thought to have occurred in the Lower Oligocene. The central stock at that time probably possessed the following characters: skull similar to that of *Elgaria*; dorsal osteoderms as in *Barisia*; cephalic scutellation much as in *Gerrhonotus l. infernalis*; body scales moderately numerous, extensively carinated, much as in *Barisia moreleti*; general color pattern similar to that of *Barisia moreleti* and *Elgaria c. coerulea, i.e.*, a longitudinal light band dorsally, and black white-tipped scales laterally, irregularly arranged; belly rather strongly mottled; postero-ventral surfaces of forearms and shanks nearly agranular; tail moderate in length.

One section of this stock became modified at the center of dispersal; the pterygoid teeth were reduced; there was some reduction of the loreo-canthal group of head plates; the postero-ventral surfaces of the forearms and shanks became more granular. These and other minor modifications produced a "*Barisia* prototype" stock in this central area. Continued modification in and southward emigration from this area produced the present arrangement of forms within the genus *Barisia*.

There was a correlated northward emigration of an essentially unmodified portion of this stock into the mountains of the border region; this represents the ancestral *Gerrhonotus-Elgaria* population. Here was developed the strong lateral fold, the tendency towards smoother and more acutely keeled osteoderms, and the generally lighter, transversely arranged color pattern, which are characteristic of those two genera. In a further emigration from this secondary center, possibly still during the Lower Oligocene, one portion of this stock became established in southern Texas, where the few modifications characteristic of *Gerrhonotus* were developed, and from whence that genus spread southward. In the group remaining in the border region the inter-

nasals and postrostrals were lost and the amount of dark pigment on the belly greatly reduced; these and other lesser modifications produced the *Elgaria* prototype stock. That region then became the dispersal center of the genus *Elgaria*.

It is to be noted that the postulated emigrations could for the most part have occurred without any necessity for crossing any extensive areas of low altitude. The most notable exceptions are found in the establishment of the genus *Gerrhonotus* and in certain groups of the genus *Elgaria*. It is in these same groups, and no others, that living representatives occur with habitats in low altitudes.

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The Loci of Contact Chemoreceptors in Insects

A Review With New Evidence[1]

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Introduction

Biologists have long known that many insects possess a contact chemical sense which enables them to distinguish edible materials from non-edible. Only recently, however, have attempts been made to discover experimentally the location and nature of the receptors involved. It is obvious that this knowledge is important for those engaged in the physiological study of the senses of insects and the mechanism of food selection by insects. Hayes and Liu (1947) further emphasize the possible importance of a knowledge of the location of chemoreceptors in understanding the action of insecticides, such as DDT. Accordingly, a study on the location of the contact chemoreceptors of insects from nine orders was undertaken to add to our meagre knowledge in this field. Further, a review of the literature to date seemed appropriate at this time, since the experimental results of the past few years and the results of this study make much of the older work of historical interest only. A description of the results of this work and a summary of our knowledge to date are here presented.

Historical Review

From the earliest times men have noted that many insects select their food carefully, and this has led naturally to the conclusion that they possess a sense of taste. Lehmann (1798) refers to Aristotle's statement of this fact. The earliest conjectures as to the location of the taste-organs were based on the belief that these organs must be in or near the mouth. Thus, Lehmann (1800) noted that a biologist, whom he does not identify, had stated that the antennae might be for taste, and this Lehmann considers too ridiculous to consider seriously. Lesser (1742) stated that the palpi were probably the seat of this sense in insects, though he offered no proof. Later, Treviranus (1816) and Dufour (1826) restated this belief.[2] Kirby and Spence (1828),

1 We are happy to express our appreciation to the following persons: Mrs. Bonnie R. O'Neal, who assisted with some of the experiments, Mr. C. L. Hamrum, who aided in many phases of the work, Prof. E. J. Anderson, who kindly furnished the honey bees used in the experiments, and Mr. R. S. Beesé, who took the photomicrographs. The expenses incurred in the photographic work were met by a grant from the John Vogel Memorial Fund of the Pennsylvania Pest Control Operators' Association.

2 According to Kirby and Spence (1828) and Plateau (1885), Lehmann (1798) credited Knoch with the statement that the labial palpi of insects are for taste and the maxillary palpi for smell. Many later workers copied this, some citing one of Lehmann's other two papers (1799, 1800) as the references. In the first of Lehmann's papers (1798), he discusses both taste and smell in insects, but without mentioning any work by Knoch; in the second (1799), he did not discuss the palpi at all; and in the last (1800), he discussed only the possibility that the antennae may be for taste. We have not been able to find anywhere in these three papers reference to any work by a Knoch or to the idea mentioned by Kirby and Spence and Plateau.

however, considered the palpi as organs of touch and the "tongue," being like the tongue of vertebrates, as the seat of taste in insects. Newport (1836) concurred in this, pointing out that the palpi are unsuited for taste because of their hard covering. He did, however, note that papillae on the proboscis of the butterfly, *Vanessa atalanta,* might be for taste.

In the years, 1860-1885, some morphological studies with a few crude experiments were reported, culminating finally in the work of Will (1885). Packard (1878) for the Rocky Mountain locust, maintained that the tips of the palpi might bear taste-organs, basing this opinion purely on anatomical considerations. Graber (1877), however, believed that one should look only in the mouth of insects for taste-organs, though he admitted that the hypopharynx might serve.

For the Lepidoptera, Müller (1877) described a group of organs at the tip of the proboscis of a butterfly which he called "Schmeckstifte." Chatin (1880), likewise, regarded the small hairs along the proboscis as possibly gustatory. Breitenbach (1882), however, disputed the statement of Müller, believing that the organ at the tip of the proboscis of the butterfly is a boring organ. He cited Graber's statement that the taste-organs of insects must be in the mouth cavity. Kirbach (1883) then described a group of papillae on a chitinous plate in the upper pharynx and called these the taste-organs. There was no experimental evidence for any of these statements.

For the Diptera, Lowne (1870) stated that, in the blow fly, *Calliphora vomitoria,* organs on the palpi, and papillae found on the labella between the pseudotracheae (interpseudotracheal papillae) are the taste-organs. This statement was based solely on the fact that the position of these seemed appropriate. Meinert (1881, 1882) accepted, with some question, the interpseudotracheal papillae as taste-organs, but believed also that hairs and papillae on the labrum, epipharynx and ligula of some Diptera (*Asilus, Tipula, Rhingia*) were possibly important. Becher (1882) likewise cautiously stated that the labral hairs of *Tabanus,* Syrphidae, etc. might be for taste. Contrasting with these cautious statements, Künkel and Gazagnaire (1881) claimed unequivocally, on purely morphological grounds, that short hairs on the epipharynx, hypopharynx, and pharynx of Diptera are the receptors, though they credited the labellar organs in an off-hand way. Kraepelin (1882, 1883), however, disagreed with Meinert and Künkel and Gazagnaire and stated with no more proof than they, that the hairs of the labella are tactile and the interpseudotracheal papillae are gustatory.

For ants, Meinert (1860) described organs on the maxillae and at the base of the tongue which he thought might be for taste, though he cautiously added a question-mark. Forel (1874, 1884), after showing that ants refuse honey to which strychnine and morphine are added, concluded, without further evidence, that the organs described by Meinert, and found by Forel at the same loci and also at the tip of the tongue, are the taste-organs.

For bees, Wolff (1875) believed that the taste-organs are in the groove of. and at the base of the tongue, and in the pharynx. He further described a

group of cup-like organs at the base of the tongue which he thought were olfactory, likening the proboscis to the nose of vertebrates. Later workers, however, discarding his crude anthropomorphism, selected these as the gustatory organs. Forel (1878) showed the error of Wolff's belief that the organs at the base of the tongue are olfactory by experiments on wasps demonstrating that the antennae are probably the loci of the olfactory organs. Later, Forel (1884) declared that the organs of Wolff in the bee are like those described by Meinert and himself in ants. Graber (1877), likewise, regarded the Wolffian organs as probably taste-organs, since they are in the mouth. Kraepelin (1882), on the other hand, returned to the tip of the tongue and described the "Borsten" at that point as taste-organs. He backed this up by claiming that these are open at the end, thus obviating the difficulty suggested by Newport that chitinous organs would be impermeable. Briant (1884), however, regarded the hairs on the tongue of the honey bee as tactile. He reported an experiment to back this up. Touching the tip of the proboscis of an anaesthetized bee with honey elicited no lowering of the proboscis. Touching the antennae, however, elicited an immediate response. He, therefore, concluded that the probocis probably bears no gustatory receptors.

In 1880, Chatin published a review in which he attempted to summarize previous work and derive some generalizations. He stated that the palpi and antennae probably do not bear taste-organs, but are for touch. He believed that the walls of the pharynx and the buccal cavity would have taste-organs, though the hypopharynx and various parts of the proboscis of Lepidoptera (hairs along the proboscis), Diptera (labella), and Hymenoptera ("tongue") might bear receptors as well. The Hemiptera, Anoplura and Siphonaptera he regarded as being without a sense of taste.

In 1877, Joseph claimed to have found sense-organs on the mouth-parts of forms from "almost all orders of insects" which he regarded as taste-organs. He also claimed to have observed color changes in protoplasm in little vesicles at the bases of these when sapid substances were brought to them. Unfortunately, Joseph did not state clearly the species of insects used in these experiments nor did he give a description of his techniques. Will (1885), therefore, questioned this work. Other workers also challenged Joseph to give full details, but he did not publish further. Thus, while this is the first description of an experimental attempt to discover the actual end-organs for contact chemoreception, there is too much uncertainty in the report for the work to be fully accepted.

Will (1885) is usually credited with starting the modern experimental approach to the study of contact chemoreception in insects. It is only fair, however, to note that the work of Joseph (1877), if his work be accepted, Forel (1874), and Briant (1884) antedated his work. Further, except for some incomplete tests with removal of palpi and unsuccessful attempts to localize the end-organs under a microscope, Will merely showed that wasps, bees, ants, and flies could distinguish acceptable materials from unacceptable on the basis of taste. It is interesting to note that, almost 100 years before, Lehmann

(1798) had likewise found that a fly would not feed on sugar which had been soaked in bitter medicine.

Will's work on the location of the end-organs, using histological techniques and assumed criteria of structure and position for taste-receptors, is no more critical than that of his predecessors. He believed that contact chemoreceptors must have the nerve-ends exposed to direct contact with sapid solutions and that the receptors must be bathed in saliva or some similar fluid. These criteria obviously eliminated the palpi and antennae as possible loci. But neither of these criteria is valid. First, so far as we know, there are no openings through the exoskeleton of the insect (Snodgrass, 1935), and thus all chemicals must penetrate (if penetration is necessary for stimulation) at least a thin exoskeletal layer to reach the nerve endings. Second, the discovery of tarsal chemoreceptors in insects (Minnich, 1921) showed that these receptors need not be bathed in saliva, if the sapid substances are already in solution. Will's "Geschmacksbecher" at the base of the tongue and the under side of the maxillae and his "Geschmackborsten" on the tip of the tongue in Hymenoptera are no more necessarily taste-organs than the supposed receptors described by other insect anatomists. While Will described the distribution and appearance of these organs only in the Hymenoptera, he wrote that he had found them in all orders of insects in similar places. The importance of Will's work lies in its summarizing, at least in part, the literature to that time and in indicating, even though crudely, the necessity for an experimental approach.

Breithaupt (1886), like Will, described pits at the base of the tongue and in the pharynx of the bees, *Bombus* and *Apis*, which he claimed to be the organs of taste. To show that the bee did not taste with the tip of the proboscis, he anaesthetized some bees and touched the tip of the proboscis with honey or sugar-water getting no response. When he touched the antennae, however, an immediate extension of the mouth-parts occurred. He concluded from this that taste-organs were lacking on the proboscis, and that taste and smell are not clearly separable in insects. It is interesting to note that both Breithaupt and Briant (1884) discovered the antennal contact chemoreceptors of the bee some time before their real recognition (Minnich, 1932). Only Briant seems to have realized, however, that these are organs of taste.[3]

Leydig (1886) disagreed with Will and Breithaupt with reference to the

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3 Forel does not seem to have believed that insects actually taste with the antennae, as Minnich (1932) so credited him. The error lies in the translation of Forel's review (1900) into English (1908). The translation, as correctly quoted by Minnich, reads (p. 96): "But in other insects they (the antennae) are mobile and serve them at once to *smell at a distance* and *taste what they can touch*" (parentheses ours). Forel's words, however, are "Mais chez d'autres insectes elles sont mobiles et leur servent à la fois à *flairer de loin* et à *tâter ce qu'ils peuvent atteindre*." Since nowhere else does Forel use the verb, "tâter," to mean taste, and in two other places at least speaks of "odorat au contact" in connection with the antennae, it seems certain that he did not believe that insects actually taste with these appendages. This is further supported by the statement of Lubbock (1888, p. 39) that no one "has suggested that the antennae are organs of sight or taste." Forel's (1886) review, which was simply republished without change in 1900 and translated in 1908, is cited in Lubbock's bibliography and thus had been read by him.

structure of the taste-organs. He believed that the hair-organs, "Tastborsten," acted for both touch and taste, depending on position, and claimed to have shown previously (1859) that the hairs on the tongue of the bee are the taste-organs, chiding Will for not finding his previous work.

Vom Rath (1887, 1888), on the other hand, agreed with Will on Hymenoptera and with Kraepelin on Diptera, coining the term, "Geschmackskegel," for the organs they had described. He believed that these are the same morphologically on the antennae, palpi, labium, maxillae, epipharynx and hypopharynx. He further stated that those on the antennae and palpi are for smell, and those on the other regions of the mouth-parts are for taste, admitting freely that he had no experimental data for this belief.

Lowne (1890), in a later edition of his book on the blow fly, also accepted Will's work, and redescribed the hairs on the palpi, which he had previously stated were gustatory (1870), and on the labella to meet the new criteria. Thus, he found these hairs grooved on the side. He discarded the inter-pseudotracheal papillae as chemoreceptors, believing that they are the openings of glands.

Gazagnaire (1886a and b), also using the criteria laid down by Will, declared that the end-organs in the Dytiscidae (diving beetles) and certain other families of water-beetles are on the posterior surface of the labrum. He performed no experiments to support this. Packard (1889a and b, 1898), likewise, "located" the taste-organ of mandibulate insects on the labrum-epipharynx without experimental support. He coined the word, "taste-cups," for the supposed end-organs and studied their distribution in insects from many orders.

At this time, the palpi of the insects reached a new low in the estimation of biologists. Plateau (1885, 1887) studied the feeding behavior of earwigs, roaches, grasshoppers and beetles and declared that, since the insects could feed normally after removal of the palpi, the palpi are useless. According to him, they are merely degenerate cephalic legs, and the insects could get along without them very well. These findings, of course, further strengthened the belief that the taste-organs of insects must be in the mouth, as Will had stated. Wassmann (1889), however, came to the defense of the palpi with a criticism of Plateau's work. He pointed out that proper controls were lacking in the experiments, and he performed some experiments in which he found that the feeding of insects from which he removed the palpi was severely affected. It does not follow, anyway, he pointed out, that the palpi are useless merely because an insect can manage without them. Wassmann believed that the palpi function at least for moving the food to the mouth-parts and probably for touch and taste, since they are well furnished with sense-organs.

Forel (1886, 1900, 1901, 1908),[4] Lubbock (1888), and Jourdan (1889),

4 Forel's review on taste was written and first published in 1886. It was republished in 1900 and translated into English in 1908. This review, however, contains no references to work after 1886.

in their reviews of the subject, summarized the work. They noted the many gaps and the great amount of controversy in the field, but generally agreed that the taste-organs of insects must be looked for in or near the mouth (pharynx, epipharynx, "palate," maxillae, etc.) and not on the palpi. The end-organs, they thought, are probably modified hairs, or the cups described by Wolff and Will, or both. All agreed, however, that the situation left much to be desired.

By far the most important contribution to the field of location of contact chemoreceptors in insects during the nineteenth century was that of Nagel (1892, 1894). He reviewed the previous literature in the field, and, on the basis of that and his own experiments, he propounded some generalizations which still have pertinence. He believed that the olfactory and gustatory organs are closely similar in function and structure, and indeed that one might function for the other. He stated that it was not necessary to have the exoskeleton perforated for stimulation, thus stating a generalization which has only recently become generally accepted. He further classified the organs of taste into inner and outer types, the inner organs inside the mouth and outer elsewhere. He believed that inner taste-organs are present in all insects, being the only ones present in mandibulate insects. Outer taste-organs, however, he stated, are found in sucking insects, and in aquatic forms, taking the place of the sense of smell. The most constant position for the inner taste-organs, Nagel wrote, was the mouth and "Gaumen," the "Kegel" or "Zäpfchen" of these regions being the end-organs. The outer taste-organs, he wrote, are usually at the bases of the palpi, tip of the hypopharynx and tip of the labium.

Nagel performed physiological experiments on *Dytiscus* larvae and adults, offering them balls of absorbent material soaked in food and food to which quinine and the like were added. The reactions of the beetles were noted before and after removal of the antennae, palpi, labrum, and other parts. From these experiments he concluded that the taste-organs of the adult *Dytiscus* are on the "Gaumenplatte" and at the bases of the labial and maxillary palpi. He believed that the larvae, however, have taste-organs on the tips of the palpi, and no inner organs. Unfortunately, all his operations were gross removals of parts, and his decisions as to the end-organs on the parts he found to bear chemoreceptors were dictated by the preconceived notion that the receptors were the type of end-organ he selected before the experiments.

Nagel performed similar, though far less thorough, experiments on other beetles and concluded that the situation was like that in *Dytiscus*. For other mandibulate insects he believed that the taste-organs are in the mouth, as in beetles, though he admitted he could find no inner taste-organs in some of these (*Periplaneta americana,* for example). For the Hymenoptera, he accepted the work of Will and Forel, redescribing their organs as "Geschmackskegel" or "Gesmackszäpfchen" and showing that these were not perforated, as Will had assumed. For the Diptera, he accepted Kraepelin's work, describing the interpseudotracheal papillae as "Geschmackskegel," and, in this

order, he found no inner receptors at all. He noted that blow flies with the antennae removed would drop the proboscis when walking over droplets of honey as soon as the feet touched the liquid. He failed to interpret this observation of tarsal chemoreception correctly, however, stating that the fly probably smells with the proboscis. For the Lepidoptera, he found no inner organs present, and noted that the "Zäpfchen" on the surface of the proboscis are probably for touch, but could be for taste, possibly being dual purpose receptors. Later (1897), after reading Kirbach's paper (1883) on butterflies, he reexamined the ventral wall of the pharynx and found there the rudimentary inner taste-organ which, from his hypothesis, he had postulated would exist.

The work of Nagel is a combination of astute experimentation and good anatomical work. Unfortunately, his experiments were often carried just short of that necessary for the attainment of his goal, and he occasionally interpreted his results to suit preconceived ideas. He did admit, though, that his experiments did not prove unequivocally the gustatory function of his supposed receptors. His experiments, however, showed more than just the fact that insects can select their food by means of a chemical sense. He further showed the futility of attempting broad generalizations from studies on one species, stating clearly that many of the arguments of earlier workers were due to their using different species, often even from different orders, without regard for the differences one should expect among animals with such widely varied food-habits as insects have.

In spite of the fact that Nagel's work clearly showed the value of the experimental approach, some workers still continued to describe parts as gustatory without experimental evidence. Thus Wesché (1904) stated that the taste-organs of *Vespa, Blatta, Apis,* and *Panorpa* are blunt hairs or pegs, in pits or on bases, on the mouth-parts. He believed that the interpseudotracheal papillae of Diptera are actually modified taste-hairs, and that the palpi of Diptera are for touch, smell, and taste. These statements were made without experimental support. Hewitt (1907, 1910, 1914) regarded the bristles at the margins of the labella and the interpseudotracheal papillae of the house fly, *Musca domestica,* as the end-organs for taste. He described a channel along the side of the bristles which communicated, according to him, with a nerve-cell at the base, and found at the tip of the papillae an opening leading into a "fine duct which ends in a pyriform sensory bulb." These organs he believed to be for taste, but he had no experiments, and his discoveries with respect to the channels and ducts seem questionable now.

Röhler (1906), after reviewing the German work on the subject, described the "Borsten" on the labium of the grasshopper, *Tryxalis,* as taste-organs. He believed that there are probably other taste-organs in the mouth, which he felt could not be differentiated from ordinary tactile hairs. Berlese (1909), likewise on purely morphological bases, assigned a gustatory function, or, rather, a combined gustatory-olfactory function, to various types of innervated hairs for insects in general. He designated trichoid, basiconic, and coeloconic sen-

silla as probably chemoreceptive, assigning a contact chemoreceptive function to those on the mouth-parts and in the mouth. Actually he simply described the possible receptors and did not show that any specific one or all are chemoreceptive.

Wheeler (1910), likewise on morphological grounds, supported by the experiments of Forel already discussed, decided that the taste-organs of ants are on the galeae of the maxillae, the tongue, and possibly the palpal tips. Forel (1921) himself later restated his beliefs, and redescribed his experiments and those of Will to back them up.

Hochreuther (1912) made a detailed morphological study of the sense-organs of the diving beetle, *Dytiscus marginalis*, and his results were later incorporated into the monograph on this species by Korschelt (1923). In general he agreed with Nagel, describing the organs which he regarded as gustatory as "Geschmackszäpfchen." In the larva, he "found" taste-organs on the tips of the antennae and palpi, the mandibles, and the maxillae. In the adult, he did not differentiate between taste and smell and described pit-pegs widely scattered over the body as possibly chemoreceptive. Near the mouth, he regarded the epipharyngeal "Zäpfchen" as most important, with similar organs on the palpal tips, and the mandibles and maxillae. These observations were not supported by any experimental work.

Bugnion and Popoff (1911), Awati (1914), and Davidson (1914) on equally anatomical grounds, described, for certain Hemiptera and Homoptera, supposed taste-organs on the hypopharynx, epipharynx, or wall of the pharnyx. These statements were based on the fact that these parts seemed to them to be correctly located for taste-organs and are equipped with structures which seemed suitable for taste.

In 1916, McIndoo performed experiments like those of Will, using the honey bee as the subject. He fed the bees honey candy, contaminated with salt, quinine, acids, peppermint oil, whisky, etc. Most of the contaminated samples were refused by the bees, and from this work he concluded that the bees possess, on the mouth-parts, a chemical sense which enables them to distinguish between acceptable and unacceptable items of diet. He then studied the sense-organs on the mouth-parts to find a possible receptor. There were only three types present—spine-like hairs, peg-like hairs, and "olfactory pores" (campaniform sensilla). He stated that, since the hairs have chitinous walls, they cannot function as chemoreceptors, for the sense-cells of chemoreceptors must be exposed directly to the stimulating substance. Therefore, he decided, there must be no sense of taste in the bee, the selection being due to an extremely fine sense of smell, mediated through the campaniform sensilla which he believed he had shown to be "olfactory pores" (McIndoo, 1914). This idea he later restated in his review (1920) on the senses of insects. His experiments, however, merely proved that the bee can select its food through some chemical sense, and only the experiments in which non-odorous substances were used are applicable so far as taste is concerned. As Snodgrass

(1925, p. 63) puts it: "Most entomologists, probably, will not be convinced by this form of reasoning that insects do not taste, since it places too much reliance on a personal interpretation of the functional possibilities of an observed anatomical structure."

The modern experimental period of study on contact chemoreceptors of insects dates from the work of Minnich (1921, 1922a and b), in which he demonstrated the presence of tarsal contact chemoreceptors in the butterflies, *Vanessa atalanta* and *Aglais antiopa*. Through a series of ingenious experiments with butterflies which were immobilized by having the wings clipped together, and using the extension of the proboscis as an index of reception, he established the presence of contact chemoreceptors on the distal part of the first segment and the distal four segments of the tarsi. His work is the first study on the location of gustatory receptors in insects in which exact observation of the reactions of the animals was possible and in which there was control of stimulation by odors and water vapor. The tarsal receptors of butterflies, he found, enable the insects to distinguish sugar solutions and other solutions from water. They, therefore, seem to be common chemical receptors at least, and probably truly gustatory. Here, at last, the search for the taste-organs of insects was broadened and put on a firm experimental basis. The stultifying hypotheses of the earlier anatomists with respect to location and structure were obviously disproved.

This does not mean that all attempts to designate specific sensilla as gustatory after this were supported by experimental work. There was, however, an increased caution on the part of insect anatomists, and most admitted that they were actually describing only possible receptors, the true nature of which would have to be determined experimentally.

Typical of this cautious approach are the papers of Taylor (1931) on Tenthredinids, Henig (1931) on lepidopterous larvae, McIndoo (1931) on the Mexican bean beetle, Hertweck (1931) and Strasburger (1935) on *Drosophila melanogaster*, Welsh (1937) on dipterous larvae, and MacGill (1947) on the bug, *Dysdercus*, all of whom described sensilla on the mouth-parts which they declared could function as gustatory receptors. They admitted, however, that these were merely possibilities, not proved.

Graham-Smith (1930), on the other hand, designated the interpseudotracheal papillae on the labella of the blow fly as "gustatory papillae," with no experimental evidence. He did not fully accept Hewitt's designation of the labellar setae as gustatory, even though Minnich (1926b), apparently unknown to Graham-Smith, had already demonstrated that the hairs on the labellar margins are taste-organs in *Phormia regina*. Similarly, Weber (1928) declared, without experimental data, that an organ on the inner wall of the labrum and the pharynx of Hemiptera is the taste-organ. Later, Weber (1933) repeated this and stated that sensilla, like those found to be gustatory in other insects, at the tip of the proboscis of bugs are for smell at close range and not for taste. Elson (1937) likewise, described on the dorsal

wall of the pharynx of various species of Hemiptera a "group of sensory cells or glands which lead into the pharynx and function as organs of taste (the gustatory organs)." Since these workers did not support their off-hand assignations of gustatory functions to organs by experimental proof, their work cannot be accepted as indicating more than possible receptors.

Demoll (1917), Snodgrass (1926, 1935) and Deegener (1928) have published reviews on the morphology of insect sense-organs (sensilla). These reports are strictly morphological and, as such, are valuable as indicating the range of forms and positions of the types of sensilla. The authors did not claim to have established any general chemoreceptive type of sensillum, but suggested that the thin-walled trichoid and basiconic sensilla may be the contact chemoreceptors. Snodgrass further noted that the sensilla which are possibly chemoreceptive are innervated by a group of nerve-cells instead of by a single cell, as in the types which are probably tactile. All these reviews stated clearly the difficulty encountered in separating insect sensilla into clearly limited structural groups.

From the standpoint of experimental work on the location of taste-organs in mandibulate insects, the Coleoptera have been best studied in recent years. Schaller (1926) observed the behavior of dytiscid beetles, before and after removal of various organs and combination of organs, after training the animals to respond to sapid substances. He concluded, from this work, that inner taste-organs are present in the mouth and outer taste-organs on the maxillary and labial palpi. Ritter (1936) and Bauer (1938), likewise using critical experimental methods, concluded that, in the water-beetle, *Hydrous,* inner taste-organs are present in the mouth and outer organs on the tips of the labial and maxillary palpi, though Ritter found the organs on the labial palpi responsive only to acids, when the maxillary palpi were removed. Warnke (1931), also using the method of removal of suspected organs, concluded that the taste-organs of two species of scarabeid beetles of the genus, *Geotrupes,* are on the tips of the maxillary and labial palpi, being either the "Kegel" or the "Zäpfchen" located there. Other taste-organs, he decided, are probably present, since abolition of the palpi did not completely abolish feeding, though the food had to be held for some time against the mouth-parts to bring about biting after the palpi were removed. Valentine (1931) likewise concluded for the beetle, *Tenebrio molitor,* that the peg-like sensilla at the distal ends of the palpi have a gustatory function. He reached this conclusion as a result of an experimental study of feeding before and after removal of the palpi.

Crombie (1941, 1944), on the other hand, stated that his experiments on the beetle, *Rhizopertha dominica,* showed that the palpi do not bear chemoreceptors. Since, however, he stated that these beetles do not find food by taste, and he studied their ability to find food, he apparently restricted the term, "chemoreceptors," to distance receptors. In the second paper of this series (1944), he described the tips of the labial and maxillary palpi, figuring sensilla like those found to be contact chemoreceptors by Schaller (1926), Ritter (1936), Bauer (1938), Warnke (1931), and Valentine (1931), but

stated that they are probably tactile, since his experiments failed to show that they were "chemoreceptive." His experiments definitely did not show that these sensilla may not be tactochemical organs, and his use of the term, "chemoreceptive," in this restricted sense is somewhat confusing.

A later study by Crombie and Darrah (1947) on the chemoreceptors of the wireworm showed that the biting response of this animal, which would most likely be the response elicited by contact chemical stimulation, requires receptors on the ligula and galeae. Their statement that "the minute projections on the tips of the labial and maxillary palps are not necessary for this response" is confusing, for, in none of the reported experiments, were the ligula and galeae alone removed. The palpi were removed in all cases with the ligula and galeae, and thus their experiments actually leave the role of the palpi undecided. The conclusion that the palpi bear contact chemoreceptors is, therefore, as justifiable as their indirect suggestion that they do not. Critical extirpation experiments or local stimulation tests like those to be described herein should easily settle this point.

Kunze (1933), after a careful study of the antennal contact chemoreceptors of the honey bee, found antennal receptors absent in a cerambycid beetle, *Rhagium* sp., and the cricket, *Liogryllus campestris*. While these animals showed no feeding reactions at all when the antennae were touched, touching the tips of the palpi brought about chewing movements.

Frings (1946), in incidental observations made during a study of the sense of taste of the roach, *Periplaneta americana*, found that the tips of the palpi are sensitive to sapid substances, but other receptors seemed to be present either elsewhere on the mouth-parts or in the mouth or pharynx.

In the Lepidoptera, Minnich's work on tarsal chemoreceptors of butterflies did not go unchallenged. Verlaine (1927) first attacked it on the basis of experiments he performed with the cabbage butterfly, *Pieris rapae*. He believed that the proboscis extensions obtained by Minnich were responses to water vapor, viscosity of the solutions, or mechanical stimulation. Minnich (1929b), and Weis (1930), however, have answered these objections very cogently. Minnich noted that, in Verlaine's work, the nutritional state of the animals, particularly with respect to water, was not controlled. This is, of course, of first importance. Weis (1930) and Anderson (1932) showed that cabbage butterflies are difficult experimental subjects, because of their erratic responses to water vapor. Even after being given all the water that they will drink, some individuals give proboscis responses when brought near water. It now seems that Verlaine's objections have been well answered, and indeed he has not pressed them further.

It is fair to conclude with Minnich (1921, 1922a), Anderson (1932) and Weis (1930) that tarsal contact chemoreceptors are present in various butterflies—the nymphalids, *Vanessa atalanta, Aglais antiopa, Cercyonis alope, Phyciodes tharos, Basilarchia archippus, Danaus plexippus*, the papilionids, *Papilio ajax, Papilio machaon*, the lycaenid, *Heodes thoe*, and the pierid,

Pieris rapae. Weis reported the following species of moths as unresponsive to tarsal stimulation—*Macroglossum stellatarum, Acherontia atropos, Sphinx pinastri,* and *Aglia tau*. Both Minnich (1929b) and Weis (1930) agreed with Verlaine that the proboscis, or the mouth itself, or both bear other taste-organs which are important in acceptance or rejection of solutions by the animals, but neither located these further.

McIndoo (1929) also challenged Minnich's work on the basis of his previous studies on the honey bee (1914, 1916). He found no organs suitable for reception on the tarsi of butterflies, since he excluded hairs as possible receptors. He did, however, find "olfactory pores" on the tarsi, and concluded that the tarsal chemoreceptors were these, and that taste was not involved, since these pores were olfactory. Once again he stated that the sensilla for chemoreception must have pores through which the nerve endings could reach the outside.

Eltringham (1933b), on the other hand, accepting Minnich's and Weis's work, described some possible end-organs on the tarsi of *Vanessa atalanta*. These are thin-walled hairs found ventrally near the distal ends of the tarsal segments of the middle and hind tarsi. They have terminal threads entering them from sensory cells and running to the tips. He found them in other species, as well, even in one which did not feed in the adult state.

For lepidopterous larvae, (*Isia isabella, Euchaetias egle*), which are mandibulate, Dethier (1937) reported that gustatory receptors are on the epipharynx and hypopharynx. These he found by stimulating the individual mouth-parts with sucrose and salt solutions on needles, following control tests with dry and moistened needles. He also studied feeding behavior before and after removal of parts. Dethier did not manage to decide on the end-organs involved in this, suggesting that the sinus organs on the epipharynx might function but he could find only long and short spines on the hypopharynx.

The discovery by Minnich of tarsal contact chemoreceptors in Lepidoptera led naturally to a search for these in other haustellate forms. Minnich (1926a) first reported them for three species of blow flies, *Phormia regina, P. terrae-novae,* and *Phaenicia sericata*. He showed that the tarsi of these forms are sensitive to water and to sucrose solutions, and that receptors are present on the labella as well. The reaction used as an index of reception was the proboscis response. It is interesting to note that Nagel (1894), and Barrows (1907) had both earlier observed the dropping of the proboscis of flies when the tarsi contacted sugar solutions, but neither interpreted the observations correctly nor made any study of these receptors.

Abbott (1928) extended the observations on tarsal chemoreceptors in Diptera to include the screw-worm fly, *Callitroga macellaria,* and showed by his experiments that urea was avoided on tarsal contact by the flies, thus indicating that the organs are capable of distingushing between acceptable and unacceptable substances.

Minnich (1929b) later published a report of extensive work on the tarsal receptors of the blow fly, *Calliphora vomitoria*. He used flies which, as in his previous work, were mounted alive by being fastened on wax blocks on the ends of wires. Thus the animals were under careful control, and their nutritional states could be accurately controlled. By means of operations, he located the receptors on the fore leg, finding them "present throughout the tarsus and at least the distal portion of the tibia," apparently confined to the ventral surfaces. He made no effort to describe the possible end-organs, but did study the physiology of reception by these organs in some detail.

Soon tarsal receptors were reported for other species of flies. Krijgsman (1930) observed that stable flies, *Stomoxys calcitrans*, when sated with water, would drop the proboscis when the tarsi touched horse serum on filter paper, though the odor alone elicited no reaction. Hertweck (1931) mounted *Drosophila melanogaster* and tested like Minnich for tarsal receptors. He found them present and found that the flies could distinguish between sugar-water and sugar-water to which he added poisons. Crow (1932), using methods exactly like those of Minnich, studied the tarsal receptors in *Calliphora vicina* (*C. erythrocephala*), *Cynomyopsis cadaverina*, and two other species of blow flies previously studied by Minnich. Haslinger (1935) also made a detailed physiological study of these receptors in *Calliphora vicina* for which their presence had already been reported. Dethier and Chadwick (1947) and Chadwick and Dethier (1947) did likewise for *Phormia regina*. Deonier and Richardson (1935) and Deonier (1938, 1939a, b, and c) extended observations on tarsal receptors to include another species of screw-worm fly, *Callitroga americana*, and the house fly, *Musca domestica*, and they studied the physiology of reception by these organs. Frings and O'Neal (1946) reported the presence of tarsal receptors in female horse flies, *Tabanus sulcifrons*, finding them on the "ventral sides of the four terminal segments and distal half or two-thirds of the first segment of the three pairs of tarsi." They believed that the receptors are medium-sized hairs found among the longer hairs on the tarsi. This was checked by touching individual hairs.

That tarsal receptors may not be present in all Diptera is suggested by the work of Middlekauf (1941) with the fruit flies, *Rhagoletis pomonella*, *R. fausta*, and *R. cingulata*. He found that these were unresponsive to tarsal contact with a "10% honey solution," though they responded when this was touched to the mouth-parts. Since, however, he did not use solutions of known concentration, and since he did not test the flies throughout starvation, his work cannot be considered as conclusive.

The presence of tarsal receptors in Diptera has not gone without challenge. McIndoo (1934, 1938), after his criticism of Minnich's work on butterflies, turned to a study of blow flies. He claimed (1934) to show that the "olfactory pores" distributed widely over the body of the blow fly, and not organs on the antennae and palpi, are the olfactory receptors. He then stated that these pores on the tarsi are the organs studied by Minnich and others, and that the insects distinguish the solutions by the sense of smell and not taste.

He performed some experiments which he thought showed that the proboscis response obtained on tarsal stimulation resulted from combined tactile and olfactory stimulation. He touched the tarsi with a needle or placed them on a piece of screening, while sugar-water was held either on a brush or in a watch glass about 3 mm. below, and not in contact with, the tarsi. These stimuli yielded a reaction about half of the time they were applied to the tarsi. Thus, he concluded, the proboscis response was due to combined olfactory and tactile stimuli, the olfactory stimuli being received through the "olfactory pores" on the tarsi, the tactile through the tarsal hairs. As previously, he declared that the tarsal hairs would be impermeable—even possibly unwettable —and that only the "olfactory pores" had the nerve-ends exposed to the outside.

This criticism, however, has been set aside by further studies. Deonier (1938), using *Musca domestica,* could not duplicate McIndoo's results at all and concluded that the tarsal receptors are really contact chemoreceptors. We, too, without formally reporting it, have tried these experiments with *Phormia regina* without checking McIndoo's work. Frings (1941) showed, through experiments in which blow flies were trained to respond to odors, that the olfactory end-organs of this form are on the antennae and labella. This eliminates the campaniform sensilla as "olfactory pores" in this form. Dethier and Chadwick (1947) later checked this with *Phormia regina.* Frisch (1921), Marshall (1935a) and Frings (1944) also showed that the olfactory organs of the honey bee, on which McIndoo's (1914) most extensive work was done, are on the antennae only. This eliminates the "pores" from consideration as "olfactory" in this species. Further, Pringle (1937a and b) has demonstrated, through electrophysiological studies, that the campaniform sensilla are really proprioceptive. McIndoo's experimental results seem probably to be due to lack of control of the state of water satiety of the insects he tested. It seems fair to conclude that his criticism is unjustified, and that the original interpretations of Minnich are correct.

Hayes and Liu (1947) have recently described hairs on the second to fifth segments of the tarsi of *Musca domestica* which, by their innervation and their position, seem well suited to be the receptors involved in tarsal chemoreception. Morphological work of the type illustrated by this study which follows and complements physiological work is a fruitful combination of the two disciplines.

There has been less done on the receptors of the mouth-parts of flies than on those of the tarsi. Minnich (1926b, 1931), Haslinger (1935) and Deonier (1939c) found these on the oral lobes, or labella, of blow flies and the house fly. Minnich (1926b) further attempted to locate the end-organs involved in labellar reception. He found that the long hairs at the margins of the labella were sensitive, that touching even one of these with a fine brush dipped in sugar-water elicited an immediate proboscis response from a fly which was unresponsive to contact with a similar brush moistened with water.

This, he correctly stated, was the first successful demonstration of a particular organ acting as a chemoreceptor.

Frings and O'Neal (1946), by touching individual hairs on the labella of female horse flies, *Tabanus sulcifrons,* with fine glass needles moistened with sugar solution, following control tests with moistened needles, showed that the medium-sized hairs among the long hairs on the labella are the contact chemoreceptors, the long hairs being tactile. The discrepancy between their results and those of Minnich (1926b, 1931) they thought to be due either to species differences or to the possibility that Minnich may have inadvertently moistened the medium-sized hairs as well as the long hairs. For the horse fly, Frings and O'Neal stated that the tarsal hairs and the labellar hairs may be the only contact chemoreceptors; at least, the tarsi and labella seem to be the sole loci of the end-organs. The only other possible end-organs in this fly would seem to be the interpseudotracheal papillae so favored by the earlier workers. Neither their work nor that of Minnich rules these out as possible gustatory receptors, but neither gives any experimental support to the belief that they are.

In the Hymenoptera, Schmidt (1938) has shown, through training experiments, that the ant, *Myrmica rubra,* has contact chemoreceptors on the antennae and mouth-parts, but probably not on the fore tarsi. She did not localize the receptors on the mouth-parts further, however. Wasps (*Polistes, Vespa*), according to Kunze (1933), along with receptors on the mouth-parts, have receptors also on the antennae.

Minnich (1932), using honey bees mounted as described before and with adequate nutritional controls, was the first to discover tarsal and antennal contact chemoreceptors in this form. The work of Briant (1884) and Breithaupt (1886) has been noted previously, but these workers failed to indicate clearly the nature of reception by the antennae, and they did not follow up their leads. Minnich noted that the tips of the antennae of the bee are sensitive, but there are so many different types of sensilla on the terminal segments of the antennae that he was not able to designate a particular type as the end-organ. He made no attempt to localize the receptors on the tarsi, except to note that he established their presence only on the fore tarsi, the middle tarsi being unsuitable for testing by his method and the hind tarsi giving questionable results.

Kunze (1933) further studied antennal contact chemoreception by the honey bee, using methods similar to those used by Minnich. He found, through removal of segments of the antennae, that the receptors are on the eight terminal segments of the flagellum. Frisch (1921) had earlier shown that these segments bear the olfactory organs of the bee, and Kunze believed that the pore-plate organs (sensilla placodea) on the antennae, which Frisch believed are olfactory, might also be gustatory. At least, he pointed out, the trichoid sensilla of the antennae are not the receptors, for drones have none of

these and their antennae are sensitive to solutions. The later work of Melin (1941) on the pore-plates puts this earlier work in a new light, but does not contribute toward the solution of the problem of exact localization of the taste organs. Marshall (1935a) also studied the tarsal and antennal receptors of the bee, but did not localize them further. In his review (1935b) on olfaction in insects, he suggested that the presence of contact and distance receptors on the antennae of the honey bee might mean that there is no separation between the chemical senses of insects, the chemoreceptors having low thresholds being usually olfactory and those having high thresholds being usually gustatory, but each capable of both functions.

An entirely new set of possibilities for loci of contact chemoreceptors in insects seems to be opened by the work of Dethier (1947), who has shown that the ovipositors of the hymenopterous parasites, *Rhyssa lineolata, Bracon* sp. and *Nemeritis canescens,* possess these organs. He was unable to decide on the exact end-organs involved, but did show that the thresholds of reaction of isolated abdomens of these forms to stimulation of the ovipositor by solutions formed series which were like those described for contact chemoreceptive responses of other insects. He concluded, therefore, that the ovipositors of these insects bear similar receptors.

During the period from 1922 to the present, the physiological work on contact chemoreception in insects and its importance for insect physiology, and comparative psychology as well, has been reviewed by Frisch (1926), Minnich (1929a), Weber (1933), Eltringham (1933a), Imms (1937), Wigglesworth (1939), Warden, Jenkins and Warner (1940), and Dethier and Chadwick (1948). These give valuable reviews on chemoreception in insects, but little on the location and nature of the receptors, since obviously little is known for sure.

The following conclusions can be drawn from the foregoing survey of the literature in this field:

1. The earlier morphological studies, where supported by no experimental work or by experiments showing merely the ability of an insect to select its food, simply indicate the possible end-organs for contact chemoreception on the insect body. They contribute little to our knowledge of the actual loci of these organs.

2. Apparently the exoskeleton of the insect is either permeable to substances in solution, or stimulation of contact chemoreceptors does not require a perforated exoskeleton, for the sensilla which have been shown experimentally to be chemoreceptive are not perforated.

3. In some Coleoptera and Orthoptera, it seems probable that the tips of the maxillary and labial palpi bear contact chemoreceptors, the basiconic sensilla found at these points being the end-organs. These are not, however, the only receptors. The galeae and ligula, at least, may bear some also, and

probably other regions of the mouth-parts as well. The antennae of the mandibulate forms may lack these receptors.

4. In some species of butterflies, contact chemoreceptors are present on the ventral sides of the tarsi; the end-organs are probably thin-walled hairs. Gustatory receptors are present also on the proboscis or in the mouth, the exact loci and sensilla involved being unknown. The larvae have contact chemoreceptors on the epipharynx and hypopharynx, but their nature is unknown.

5. In the muscoid Diptera, contact chemoreceptors are present on the ventral sides of the tarsi, the sensilla probably being thin-walled hairs. Similar trichoid gustatory receptors are present on the labella of at least two species of flies, but these may not be the only receptors on the labella. The receptors on the tarsi and labella may be the only receptors in these flies.

6. In the honey bee, besides contact chemoreceptors on the mouth-parts which have not yet been located, tarsal and antennal receptors are also present. Those on the antennae are restricted to the eight terminal segments, but their nature is unknown. Antennal receptors are also present in wasps and ants. Receptors with properties similar to those of the tarsi and mouth-parts are present on the ovipositors of some hymenopterous parasites.

7. Future attempts to find the loci of contact chemoreceptors and to locate the specific end-organs involved must take into account the possibility that these may be found, at least, on the antennae, mouth-parts including the palpi, tarsi, and ovipositor.

The experimental and morphological studies described in the following report have as their object the discovery of the loci of contact chemoreceptors in insects from all the larger orders. In some cases, the studies are incomplete, in others they merely show the difficulties involved in developing critical experimental procedures. In others, however, they are complete enough to allow us to decide on probable end-organs for contact chemoreception. It is hoped that this report will stimulate much further experimental work in this field, where so much is needed, and that insect histologists, starting with the knowledge that certain sensilla are chemoreceptive, will be able to discover the finer structure of these organs. This will immeasurably aid both the morphologists and the physiologists in their future work.

MATERIALS AND METHODS

Twenty-three species from nine orders were studied in the present work. These are summarized in the following list (the scientific and common names are from Muesebeck, 1946, where they are given there):

THYSANURA

Family, Lepismidae

Thermobia domestica (Packard)—Firebrat

75 individuals, laboratory reared

ORTHOPTERA

Family Blattidae
Periplaneta americana (Linn.)—American cockroach
75 individuals, laboratory reared
Blattella germanica (Linn.)—German cockroach
54 individuals, trapped on infested premises

Family, Gryllidae
Gryllus assimilis Fab.—Field cricket
14 individuals, captured in the field

Family, Mantidae
Tenodera aridifolia sinensis Sauss.—Chinese mantis
10 individuals, laboratory reared

Family, Acrididae
Melanoplus differentialis (Thos.)—Differential grasshopper
37 individuals, laboratory reared

NEUROPTERA

Family, Chrysopidae
Chrysopa sp.—Golden-eyed lacewing
5 individuals, captured in the field

ODONATA

Family, Libellulidae
Libellula sp.—A dragon-fly
37 individuals, captured in the field

COLEOPTERA

Family, Carabidae
Galerita janus Fab.—A ground beetle
4 individuals captured in the field

Family, Meloidae
Epicauta pennsylvanica DeG.—Black blister beetle
14 individuals, captured in the field

Family, Cantharidae
Chauliognathus pennsylvanicus DeG.—Soldier beetle
36 individuals, captured in the field

Family, Cerambycidae
Tetraopes tetraophthalmus (Forst.)—Red milkweed beetle
30 individuals, captured in the field

HEMIPTERA

Family, Lygaeidae
Oncopeltus fasciatus (Dallas)—Large milkweed bug
112 individuals, laboratory reared

LEPIDOPTERA

Family, Pieridae
Pieris rapae (Linn.)—Imported cabbageworm butterfly
25 individuals, captured in the field
Colias philodice Latr.—Clouded sulfur butterfly
15 individuals, captured in the field

Family, Danaidae (Nymphalidae)
Danaus plexippus (Linn.)—Monarch butterfly
Larvae, 8 individuals, captured in the field
Adults, 25 individuals, reared from larvae

DIPTERA

Family, Syrphidae
Eristalis sp.—Drone fly
12 individuals, captured in the field

Family, Calliphoridae
Phormia regina (Meigen)—Black blow fly
125 individuals, laboratory reared
Phaenicia (*Lucilia*) *sericata* (Meigen)—Green-bottle fly
25 individuals, laboratory reared

Family, Muscidae
Musca domestica Linn.—House fly
25 individuals, laboratory reared

HYMENOPTERA

Family, Vespidae
Polistes sp.—Polistes wasp
26 individuals, captured in the field
Vespula maculata (Linn.)—Balf-faced hornet
6 individuals, captured in the field

Family, Apidae
Apis mellifera Linn.—Honeybee
49 individuals (workers), captured in the field

All individuals used were adults, except in the case of the larvae of the monarch butterfly. Where it was simple to determine the sex, the animals were selected so as to be about half males and half females. Where sex determination was difficult or impossible, relatively large numbers and random collection usually insured approximately half males and half females in the test groups. Where only small numbers of individuals were used, it is obviously possible that members of only one sex were tested, but, except in the Hymenoptera, there was no conscious selection of one sex.

For convenience in testing, most of the insects were mounted alive, for the butterflies by fastening the wings together with a spring clothes-pin, and for all others by fastening the dorsal side of the thorax and the wings to a wax-block on the end of a glass rod. This method has been described in detail elsewhere (Frings, 1947) and will not be further discussed here. Longevity was good, if the insects were supplied with water and food regularly. Most insects lived for at least a week and many for two weeks or more. American roaches lived up to seven months thus mounted. There was no evidence that mounting them in this way rendered them abnormal in any respect.

The solutions used in the following tests were of two types—acceptable and unacceptable to the insects. As a universally acceptable solution, 1 M sucrose solution was used. As unacceptable solutions, either 2 N NaCl or 2 N NH_4Cl were used. Normal insects, when starved for a day or two, would accept the sugar solution readily, after being given all the water they would take. They would not accept the salt solutions, however, whether sated with water or not. The usual period of inanition before testing in the following work was one or two days, but, for most species, some individuals were allowed to starve to death and were tested throughout.

The matter of water satiety in tests on contact chemoreception is of first importance. Most insects, when "thirsty" exhibit active seeking movements or proboscis extensions when moist objects are brought near them. It is absolutely essential, therefore, that the insects have all the water they will take before testing with sugar-water. This alone is not enough, however, for an insect which has drunk all it will at the beginning of a series of tests often becomes responsive to water during the tests. It is necessary also that control tests, using water under the same conditions as the sugar solution is to be used, be interspersed—at irregular intervals to avoid any possible conditioning—among the taste tests. Some species—*Oncopeltus fasciatus*, and *Pieris rapae*, for instance—are quite erratic at all times in their responses to water, even when they will not drink any when offered. Obviously if a positive feeding or other response is obtained when water alone is used, it is necessary to discontinue testing with the individual that thus responds, offer it water, and then later retest for a negative water reaction.

The reactions used as indices of reception of the contact chemical stimuli varied with the insects used. In the mandibulate insects these were usually movements of the mouth-parts along with active extension of the head and seeking movements. Often these were difficult to interpret, and control tests were necessary to discover the reactions to simple contact, so that these could be distinguished, if possible, from reactions to chemical stimulation. With some species of insects—caterpillars for instance—almost anything touching the mouth-parts is sufficient to initiate vigorous chewing movements. In the haustellate insects, the proboscis, which is kept in a position of rest against the body or curled up, is extended on stimulation of contact chemoreceptors. This clean-cut proboscis response makes the haustellate forms particularly apt subjects for these tests.

Usually the first tests were for the purpose of establishing the general location of the contact chemoreceptors. For these, fine artist's brushes dipped in water and in the solutions were touched to various parts of the insect's body while the insect was observed under a binocular microscope. In many species the tarsi and antennae were also dipped in liquids in watch-glasses. These tests allowed the experimenter to determine the approximate location of the receptors, and the nature of further work depended upon the results of these tests.

For exact location, two methods of testing were used: local stimulation, and removal of suspected loci. For the local stimulation tests the insect was left intact, though some appendages might be immobilized by being fastened in the wax or drawn against the insect's body by means of a strip of paper fastened in the wax block on each side (further information about these "dresses" may be found in Frings and O'Neal, 1946). Water and solutions were brought to the parts of the insect on very fine glass needles made by drawing out narrow bore glass tubing or glass rod. The parts of the insects to be tested were touched first with a dry glass needle, followed by a glass needle moistened with distilled water. The reactions to these mechanical stimuli were noted. After that, the parts were touched with a needle moist-

ened with sucrose solution. If the parts bore receptors and if the animal were hungry, this ordinarily elicited the typical feeding reaction. The routine was varied widely, according to the circumstances, so that repeated tests were sometimes made with the control needles, before a test was made with the sugar solution, and many other similar variations. All these tests were carried out with the insect under the highest practical power of the binocular microscope. For the removal experiments, various parts were cut off and the insects were tested before and after the operations. These operations were performed under a dissecting microscope with microscalpels made from small pieces of razor-blades. Usually the insects were anaesthetized for the operation, but not always. The extent of the operation was checked with the binocular microscope and usually later by mounting the part on a microslide and examining under the compound microscope. The animals were not tested until their reactions showed them to be completely recovered from the anaesthesia.

The interpretation of local stimulation studies is often difficult. As a general rule, it seems safe to say that negative results (i.e., lack of distinctive feeding behavior following contact with sugar solutions) do not constitute proof of lack of reception, unless backed up by other data. It is possible, especially when using small volumes of fluid, as with glass needles, that an insufficient stimulus occurred. It is also possible that the reaction selected as an index of response, while elicited by contact with a galaxy of taste-organs, is not elicited by contact with a few organs. On the other hand, positive results (i.e., evocation of distinctive feeding behavior following contact with sugar solutions), if care is taken to avoid touching other parts, is an excellent indication of reception. Either of these general statements, obviously, depends on having the animals sated with respect to water and having adequate controls.

Removal experiments also are often difficult to interpret, and, indeed have often been misinterpreted, even by careful workers. Forel (1900, as translated by Yearsley, 1908 p. 104) thus described an experiment he performed: "I therefore amputated both antennae and the four palpi in several wasps. Then I gave them honey mixed with quinine. It was naturally necessary to bring them so that their mouth touched the honey, for they were not in a condition to find it alone. They then tasted it, but abandoned it each time immediately after. On the contrary, when I put pure honey without quinine or morphine, they ate it greedily. This shows that the gustatory faculty is independent of the antennae and the palpi, and that it resides in the mouth." Obviously it shows nothing of the sort with respect to the antennae and palpi. It does show that, with the antennae and palpi removed, these insects could still distinguish acceptable from unacceptable foods, presumably on the basis of a contact chemical sense in or near the mouth. The palpi and antennae, however, so far as can be decided on the basis of these experiments, may or may not bear end-organs.

Similarly, Crombie and Darrah (1947), after showing nicely that the antennae are not the loci of end-organs which are necessary for the biting response of wireworms, found that removal of the labial palpi, maxillary palpi, ligula, and galeae abolished the response. Removal of the maxillary and labial palpi and the ligula, leaving the galeae, did not abolish the response. They

concluded: "Normal biting occurs when only the galeae are present, showing that the minute projections on the tips of the labial and maxillary palps are not necessary for this response." Actually, these experiments do not show that the palpi are unnecessary for this response, for the palpi were removed in all their tests. All that is indicated is that the galeae are sensitive and that, if the palpi bear end-organs, these are not the only ones present.

Many examples of similar misinterpretation could be selected, but these two examples from the work of competent and careful research biologists show how easy it is to misinterpret extirpation experiments. As a general rule, if removal of a part does not abolish the response being used as an index of reception, the part either does not bear the end-organs or it is not the sole locus of the end-organs. On the other hand, if removal of a part does abolish the response it is possible that it does bear the end-organs. If this is supported by other experimental results, final conclusions may be possible.

When, in our experiments, it was suspected that all the contact chemoreceptors were removed by the operations, thirsty animals were given salt solutions, varied in presentation with distilled water. Normal animals, of course, took the water and refused the salt solutions. Indiscriminate acceptance of salt solutions and water was taken as indicative of lack of contact chemoreceptive capacity. For these tests, moistened artists' brushes were used instead of glass needles, so that sizeable droplets could be presented to the thirsty animals.

A further difficulty in the study of the location of contact chemoreceptors is that they seem to be present on the mouth-parts of all insects, and movements of the mouth-parts are the most usual innate reaction to contact chemical stimulation. It is thus often difficult to remove parts suspected of bearing chemoreceptors without also seriously affecting the ability of the insects to respond.

In testing any of the appendages for contact chemoreceptors by local stimulation, difficulty was occasionally experienced with the insects' bringing the parts to which the solutions were applied to the mouth-parts. With many insects this touching of the mouth-parts with moveable appendages is a source of considerable trouble. The precautions taken to avoid this varied with the species, the most usual being the use of small amounts of liquid and careful observation. When tarsal receptors were present, the movements of the legs by the insects often interfered with the testing of parts lying closer to the body. In these cases, the tarsi were usually immobilized by being fastened to the insect or were removed. In the honey bee, where the antennae bear receptors, it was necessary to remove these from the field of action in testing other parts. The collar described by Marshall (1935a) was found to be quite satisfactory for this purpose.

Tests were also made on free animals, especially in testing for tarsal receptors. The insects were placed in finger-bowls or Petri dishes with filter paper on the floor. Here they were supplied with distilled water but not food, and, in a few days, they were naturally quite hungry. It was easy to show that these animals, while not taking water and therefore unresponsive to water vapor, would eagerly take sugar-water when brought to the mouth-

parts. The testing for tarsal receptors was accomplished either by placing drops of sugar-water on the tarsi of the animals, as they stood in the dishes, or by placing drops on the filter paper thus allowing them to move by capillarity to the tarsi of the insects. As a control, distilled water droplets were similarly applied. The solutions used in this method, if they were applied as drops to the tarsi, were maintained at the same temperature as the room. If this was not done, thermal stimulation of the tarsi caused the insect either to bring the tarsi to the mouth-parts or to bring the palpi or other regions of the mouth-parts to the drops and thus to discover them without true tarsal reception.

For microscopic study of the sensilla found on the mouth-parts, tarsi, and so on, these parts were mounted whole in Diaphane on microslides. Some of these were stained with alcoholic methylene blue or with hematoxylin before mounting. No histological sections of the parts have been prepared.

RESULTS AND INTERPRETATIONS OF EXPERIMENTS

The most extensive series of experiments were made with *Periplaneta americana*. These will be presented first in some detail to show the general methods and controls used. The other forms were similarly treated, and detailed data will, therefore, be omitted and the results of the experiments summarized.

Periplaneta americana, American Cockroach.—Touching either antenna with a dry glass needle elicits withdrawal, if the antenna is touched at a distance of more than about 1 cm. from the head. Often this is accompanied by general activity, such as kicking. If the antenna is touched at a distance of less than 1 cm. from the head, the animals reach with the maxillary palpi toward the source of stimulation. Exactly the same reactions are obtained with needles dipped in water, sugar-water, or salt solutions. Continued stimulation abolishes the response through habituation, and stimulation of the antennae of roaches which are cleaning or "sleeping" results in no observable reaction. From many replications of these observations, using artist's brushes as well as needles, it seems fair to conclude that the antennae bear no contact chemoreceptors.

Touching the fore tarsi with a dry glass needle elicits either withdrawal, or more usually reaching for the needle with the maxillary palpi. With the needle moistened with water, sugar-water, or salt solutions, no observable differences are found. Often the roach tries to draw the needle to the palpi. If this is prevented, there are no feeding movements. If the animal succeeds, chewing movements start as soon as a needle moistened with sugar-water touches the palpal tips. With the middle and hind tarsi, the typical reaction to contact is withdrawal of the appendages; there are no observable differences in reaction with sugar-water or salt solutions. When other segments of the legs are touched, the palpi are moved toward the stimulated part. Contact chemoreceptors are thus probably not present on the legs.

Touching the cerci elicits only withdrawal or no reaction at all, depending on the degree of stimulation afforded, with no differences between control and test needles. Contact of the needles with other parts of the body results in

no reactions which can be interpreted as indicative of contact chemoreception. The contact chemoreceptors involved in feeding behavior, therefore, seem to be limited to the region near the mouth.

When the tip of a maxillary palpus is touched with a dry needle or one moistened with water, the palpus is withdrawn, and often the roach exhibits slight bouncing movements of the body, with movements of the legs. When the tip of this palpus is touched with a needle moistened with sugar-water, on the other hand, the roach's head is immediately extended, the palpi are waved eagerly around, and chewing movements occur. This typical reaction pattern, which is followed by feeding, if that is permitted, is useful as an index of response. It is obvious that the tips of the maxillary palpi bear gustatory receptors.

These can be more precisely located by local stimulation under a binocular microscope. Only the terminal segment of the palpus is sensitive, and that only along the ventral side of the segment near the tip. Along this side there is a special field of sensilla, ovoid in shape. This area can easily be shown to be the receptor field. Fig. 1 is a photomicrograph of a maxillary palpus of *P. americana* showing this sensory field.

With the maxillary palpi excised, it is possible to touch the labial palpi. Unless the maxillary palpi are excised, the roach brings their tips into contact with the needle as soon as it touches a labial palpus. When the tips of the labial palpi are touched with sugar-water there is an immediate feeding reaction. Local stimulation experiments showed that the receptors here were confined to the tips, in a well defined sensory field (Fig. 1). Other parts of the labial palpi, while obviously well supplied with tactile receptors, apparently do not bear contact chemoreceptors.

Fig. 1.—(*Left*) Right half of labium of *Periplaneta americana* (×22) showing the light colored sensory field at the tip of the palpus. (*Right*) Maxillary palpus of *P. americana* (×17) showing the light colored sensory field along the ventral side of the terminal segment.

With the palpal tips removed, roaches are not able to distinguish sugar-water from distilled water until it is brought into contact with the mouth-parts. Then, however, they can easily distinguish between the two, taking sugar-water eagerly, when sated with water. They can also distinguish salt solutions from water, taking the water, when thirsty, but not the salt solutions. Thus, there are contact chemoreceptors present on the mouth-parts other than on the palpal tips.

Using very fine needles, it is possible to touch specific points on the mouth-parts of a roach without touching the palpi, or the palpi may be excised and other regions thus stimulated. These experiments showed that the tip of the labium and the hypopharynx are sensitive to chemicals. To test this further, the palpi were removed and then various combinations of excisions were performed. With the palpi removed, and either the ligula or hypopharynx removed, the roaches can still distinguish sugar and salt solutions from distilled water, when brought to their mouth-parts either on a glass needle, an artists' brush or as a droplet on a small piece of glass microslide fastened to the end of a short glass rod (see Frings, 1946, for description of this piece of apparatus). With the palpal tips excised and with both the hypopharynx and the ligula removed, however, the roaches indiscriminately refuse all fluids or take all fluids, depending on their nutritional state. It would seem, therefore, that the sole loci of contact chemoreceptors in or near the mouth of the roach, are the tips of the maxillary and labial palpi, the hypopharynx, and the ligula. Animals with these parts removed take salt solutions when thirsty just as they do water, something which no normal roach does. When hungry, but sated with water, they exhibit no feeding response, even when rather large droplets of sugar solution are brought to the mouth-parts. This is true even when a long enough time is given (up to 3 minutes) for the sugar solution to reach any receptors on the epipharynx or in the mouth cavity. There seem to be no effective receptors at these places.

To test this quantitatively, thresholds for sucrose were determined with

TABLE I.—Thresholds for sucrose for the American cockroach with excisions of the parts listed.

Parts excised	No. of roaches	No. of tests	Observed range	Mean ± Stand. error
None	11	11	.028 - .057 M	0.037 ± .0025 M
Palpal tips	20	20	.018 - .090 M	0.035 ± .0041 M
Palpal tips + ligula	8	8	.018 - .057 M	0.039 ± .0060 M
Palpal tips + hypopharynx	21	31	.022 - .090 M	0.060 ± .0042 M
Palpal tips + ligula + hypopharynx	20	40	No response to sucrose solutions when sated with water*	

* Two roaches responded once each to 2 M sucrose solution, but they did not repeat this behavior.

roaches starved for 24 hours and given water to satiety. The data are presented in Table I. The slight discrepancy between the threshold reported here for normal roaches and the threshold reported previously (Frings, 1946) is undoubtedly due to the small number used here and to the fact that these were from a different group of roaches than those used in the previous work. The rise in threshold following removal of the palpal tips and hypopharynx suggests that the labial tip alone is less sensitive than the hypopharynx. It has been suggested earlier (Frings, 1946) that the palpal tips are not as sensitive as the "inner" organs. Unfortunately, roaches with the "inner" organs removed and with only the palpal tips have not been tested.

These results show plainly that, so far as the mouth-parts are concerned, the receptors for contact chemical stimulation are on the tips of the palpi, the hypopharynx, and the ligula. So far as can be determined, no other contact chemoreceptors exist on the mouth-parts or in the mouth or pharynx.

The presence or absence of tarsal or antennal receptors were also tested for by observations on unmounted roaches confined in fingerbowls, and given no food, but all the water they wanted. As the roaches moved about, the maxillary palpi were kept in active motion touching the floor of the bowl with the sensory fields at the tips. If these touched a drop of sugar-water, the roach immediately sucked it up. Merely walking through the drop of sugar-water did not bring about feeding. Drops of water and sugar-water were placed on the tarsi as the animals stood quietly in the dishes. In a few cases the roaches lifted the tarsi from the drops and brought them to the mouth-parts. These responses, however, apparently were due to differences in temperature between the fluids and the dishes, for when these were the same, it was possible to flood the feet of starving roaches with sugar-water without any sign of recognition on their part. If, however, the maxillary palpi touched the fluid, the roaches immediately began active feeding. The antennae and cerci, tested similarly seemed equally to lack contact chemoreceptors.

Free roaches with the maxillary palpi removed, after a short period of adjustment, brought the body lower so that the tips of the labial palpi touched the substrate as they walked. Sugar-water was recognized on contact with the palpi and feeding commenced. With both labial and maxillary palpi removed, the roaches seemed almost incapable of finding sugar solutions, walking through droplets indiscriminately. If thirsty, they recognized water, however, apparently through some water-vapor sense. But, if not thirsty, removal of the palpi seriously affected their finding of food droplets, provided these, as in the present experiments, were without food odor. However, if the mouth-parts of a palpectomized roach touched a droplet accidentally, feeding occurred immediately.

With all the suspected loci of contact chemoreceptors removed (palpal tips, ligular tip, hypopharynx), the roaches easily found and imbibed water when thirsty, though they also took salt solutions too, which no normal or palpectomized roach did. These roaches, however, seemed incapable of distinguishing drops of sugar-water from plain water, and thus, if sated with water, starved without feeding on drops of sucrose solution lying all around. They did, however, seem able to recognize dog-biscuit, moving the antennae actively when it was brought near them, and, if it were placed against the

mouth-parts, chewing slowly (cf. also Glaser, 1927). The recognition here apparently depends on olfactory stimuli, mediated probably through the antennae.

From the results cited above, it is obvious that the contact chemoreceptors involved in feeding behavior in the American cockroach are located on the tips of the maxillary and labial palpi, the tip of the hypopharynx, and the ligula.

Blattella germanica, German Cockroach.—All the experiments which were done with the American cockroach, except the determination of thresholds, were done with this species. The results were exactly the same. The contact chemoreceptors of this insect, therefore, are also located on the tips of the palpi, the hypopharynx, and the ligula.

Gryllus assimilis, Field Cricket.—Only experiments utilizing brushes for general location were done with this species. These showed that the antennae, legs, and cerci lack receptors, while the palpal tips and some other regions of the mouth-parts bear them. These results check those of Kunze (1933). Since excisions of the palpi were not performed, the loci of the end-organs on the mouth-parts were not determined accurately.

Melanoplus differentialis, Differential Grasshopper.—All the experiments which were performed with *P. americana,* except the determination of thresholds, were done with this species. There was no evidence that the ligula bears receptors, otherwise the situation was similar. Removal of the palpal tips, on which there are clearly delimited sensory fields, and the hypopharynx apparently abolished reception. The only contact chemoreceptors of this species seem to be on the palpal tips and the hypopharynx. It is interesting to compare this with the case of the roaches and to relate this to the differences in food habits between these two types of insect. Also, this difference in the loci of receptors between two species from closely related groups shows clearly the impossibility of using data obtained in a study on one species to postulate conditions in another.

Tenodera a. sinensis, Chinese Mantis.—The tests with this organism were incomplete, omitting excisions and determinations of thresholds. All observations were on free animals. The results showed that the antennae, tarsi, and cerci probably do not bear receptors, while the palpal tips are sensitive. Other receptors are also present, as indicated by the chewing movements resulting when the mouth-parts were touched with sugar-water, without touching the palpi. The loci of contact chemoreceptors are thus the tips of the maxillary and labial palpi and some other points on the mouth-parts.

Thermobia domestica, Firebrat.—This insect proved to be an exasperating experimental animal. Some of the individuals responded to almost any stimulation near the mouth-parts, and many more responded to sugar-water very poorly. Because of the erratic nature of the responses, results were not clear-cut, and, while many individuals were used in these tests, the interpretations are not as definite here as in the other insects tested. All the experiments done with *P. americana,* except determinations of thresholds, were tried. It is

almost certain that the antennae, tarsi and posterior bristles do not have contact chemoreceptors. The maxillary palpi are relatively long and filiform, and the labial palpi short and thick (Fig. 2). The maxillary palpi are carried extended, the labial palpi folded against the labium. Local stimulation of these showed that the maxillary palpi almost certainly do not bear contact chemoreceptors, while the tips of the labial palpi are definitely loci of such receptors. Local stimulation of the tip of the labium showed that this too was sensitive. Excisions have failed so far to elicit further information as to these receptors.

Chrysopa sp., Golden-Eyed Lacewing.—Only local contact experiments with glass needles were performed with this species. The antennae and tarsi

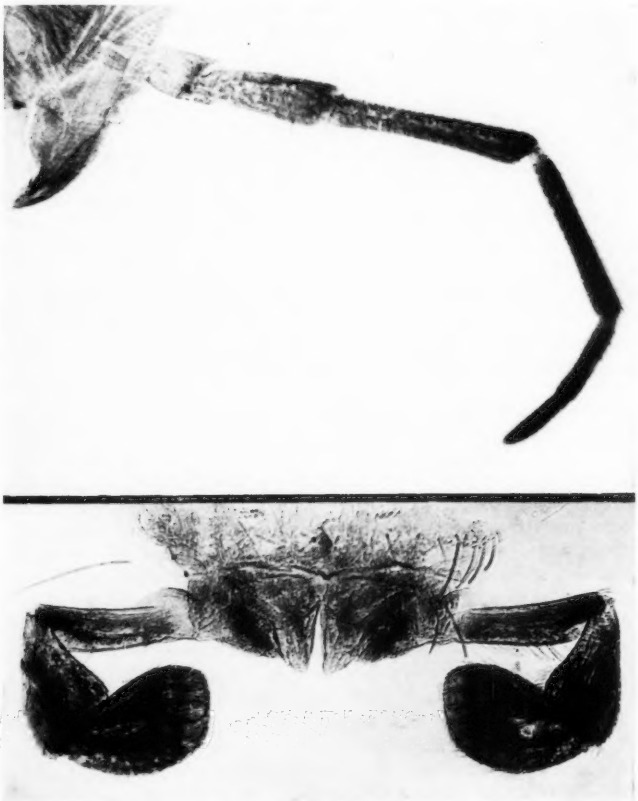

Fig. 2.—(*Above*) Maxilla of *Thermobia domestica* (×55). (*Below*) Labium of *T. domestica* (×80). Both specimens from prepared slides stained with methylene blue.

apparently do not bear receptors, while the tips of the palpi are very sensitive.

Libellula sp., Dragon-Fly.—This animal proved even more uncooperative than the firebrat. All the experiments tried with *P. americana* were done with these, except for the determination of thresholds and tests with free animals. The insects are very tight-mouthed and difficult to test locally. When sated with water, they would sometimes take sugar-water, with chewing movements. This reaction seemed at first to be a good index of reception, but it failed miserably. Often it seemed as if the dragon-fly had no receptors at all, for they would take almost anything offered to them, even 2 N NH_4Cl solution. Feeling that the presentation of droplets was not adequate, tiny balls of cotton soaked in water, sugar-water, and 2 N NH_4Cl were offered. When sated with water, some individuals rejected the NH_4Cl and water soaked balls and accepted the ones soaked in sugar-water, but others took all indiscriminately. While mounted, dragon-flies were fed on small bits of meat. If these were soaked in 2 N NH_4Cl solution, they were often taken just as readily as untreated meat. The most that can be said so far is that the antennae and legs do not seem to bear any receptors, and the mouth-parts probably do, but the exact location on the mouth-parts remains to be determined.

Galerita janus, Ground Beetle.—All the experiments tried with *P. americana* except the determination of thresholds and attempts to remove all contact chemoreceptors, were tried with these animals. The antennae and legs obviously lack receptors. The tips of the maxillary palpi (Fig. 4) and labial palpi bear contact chemoreceptors in definite fields. The tips of the maxillae and the mandibles bear no receptors, but the tip of the labium is quite sensitive. The receptors discovered thus far, then, are on the tips of the maxillary and labial palpi and the tip of the labium, but others may be present.

Epicauta pennsylvanica, Black Blister Beetle.—The results here were exactly like those with *G. janus* above. The contact chemoreceptors are on the tips of the maxillary and labial palpi, the labial tip, and possibly elsewhere on the mouth-parts.

Chauliognathus pennsylvanicus, Soldier Beetle.—A very detailed set of experiments was performed with these animals. The results will be only briefly summarized. The feeding reaction is clear-cut and quite easy to observe. It consists of opening of the mandibles and extension of the maxillae, as a proboscis-like structure. The extension occurs in two phases—1. extension of the lateral pieces, and 2. extension of the long tongue-like central parts. Reaction 1 occurs on stimulation of the palpal tips with sugar-water, but reaction 2 only occurs after some of the sugar-water has been imbibed. Touching the tips of the extended maxillae with sugar-water, water, or salt solutions elicits sucking, but water and salt solutions are rejected when a little of the material has been taken up. The receptors, obviously are not on the tips of the maxillae, but lie deeper. The antennae and tarsi bear no receptors. It seems, therefore, that the loci of contact chemoreceptors for this species are the tips of the maxillary and labial palpi and elsewhere on the mouth-parts.

TABLE II.—Summary of results of experiments on the location of the contact chemoreceptors in mandibulate insects.

Insect	Regions shown to bear contact chemoreceptors	Regions shown probably not to bear contact chemoreceptors
THYSANURA *T. domestica*	Tips of labial palpi, ligula, probably other regions on mouth-parts	Antennae, tarsi, tips of maxillary palpi
ORTHOPTERA *P. americana*	Tips of maxillary and labial palpi, ligula, hypopharynx. These are probably the only loci of contact chemoreceptors in this species	Antennae, all parts of legs, all other regions of the mouth-parts and buccal cavity than those enumerated at left, wings, head capsule, body-wall of thorax and abdomen, cerci
B. germanica	Same as for *P. americana*	Same as for *P. americana*
G. assimilis	Tips of maxillary and labial palpi	Antennae, tarsi
M. differentialis	Tips of maxillary and labial palpi, hypopharynx. These are probably the only loci of contact chemoreceptors in this species	Same as *P. americana*, with the addition of the ligula
T. sinensis	Tips of maxillary and labial palpi.	Antennae, tarsi
NEUROPTERA *Chrysopa* sp.	Tips of maxillary and labial palpi	Antennae, tarsi
ODONATA *Libellula* sp.	Somewhere on the mouth-parts (?)	Antennae, tarsi
COLEOPTERA *G. janus*	Tips of maxillary and labial palpi, ligula	Antennae, tarsi, tips of maxillae, mandibles, other parts of palpi than the tips
E. pennsylvanica	Tips of maxillary and labial palpi, ligula, other regions on the mouth-parts	Antennae, tarsi, other parts of palpi than the tips
C. pennsylvanicus	Tips of maxillary and labial palpi, other regions on the mouth-parts	Antennae, tarsi, tip of "proboscis" (maxillae), other parts of palpi than the tips
T. tetraophthalmus	Tips of maxillary and labial palpi, ligula	Antennae, tarsi, other parts of palpi than the tips

Tetraopes tetraophthalmus, Red Milkweed Beetle.—The results with this animal were exactly the same as for *G. janus.* Receptors are on the palpal tips and the tip of the labium, but these may not be all that the animal has.

Summary of Results on the Mandibulate Orders.—The results of the experiments on the mandibulate insects are summarized in Table II. These show that, where the loci of end-organs could be determined accurately, the maxillary palpi (except probably for the firebrat) and the labial palpi bear them at their tips. For the beetles, these results check those of Schaller (1926), Ritter (1936), Bauer (1938), Warnke (1931), Valentine (1931), and Kunze (1933). Other receptors are present on the mouth-parts in all. Where located accurately, these were found on the labial tip, except in the grasshopper, and on the hypopharynx. The mandibles probably do not bear contact chemoreceptors and the labrum possibly not. In those insects in which complete removal of all receptors was attempted no evidence was found to indicate that receptors exist in the mouth or pharynx. The antennae, tarsi, and cerci where present, of these forms, seem not to bear contact chemoreceptors.

Oncopeltus fasciatus, Large Milkweed Bug.—The loci of contact chemoreceptors were determined by local stimulation methods, using both brushes and needles, and by removal followed by exposure of parts to solutions in watch-glasses. This animal is not an easy experimental subject with which to work. The reactions to water are erratic and often confusing. To render the bugs negative to water, it is necessary to allow them to have all the water they wish over a period of some time, usually for more than an hour. The animals were suspended for this period over a dish full of water, and a surprising number of them kept the proboscis lowered for most of that time. Control tests with water were necessary in a ratio of three or four to one application of sucrose solution. The milkweed bug does not become reactive to sucrose solutions until after 2 or 3 days of inanition and then not all individuals respond. The reactions are slow, and consequently up to 30 seconds' periods of exposure were used.

With intact animals, it is simple to discover, by dipping the tarsi into solutions in watch-glasses, that receptors are present either on the antennae, or tarsi or both. The difficulty with using intact animals is that the fore tarsi can reach as far as the antennae and vice versa. Thus the bug almost invariably brings the fore tarsi and antennae simultaneously into contact with solutions. With the antennae removed, however, the insects can distinguish sucrose solutions from distilled water with the tarsi. Local stimulation and removal of legs, followed by dipping the remaining legs in water and solutions in watch-glasses, showed that all the tarsi are capable of reception. The segments of the tarsi which are active have not so far been discovered. With the fore legs, or fore and middle legs removed, the insects seem incapable of distinguishing sugar solution from distilled water by means of the antennae. Unfortunately, animals with these legs removed tend to hold the antennae up above the body in such a way as to make it difficult to touch them to sugar-

water in a watch-glass. Touching with a brush moistened with sucrose solution, following distilled water controls, however, elicits no proboscis response. In view of the possibility that a higher concentration of sucrose might be effective, all the experiments were repeated using 2 M sucrose solution. The results were the same. The antennae, thus, seem to bear no contact chemoreceptors.

Using glass needles, under a binocular microscope, it is possible to bring water and solutions to the tip of the proboscis without touching the tarsal receptors. At the tip of the proboscis there is visible a group of sense-organs. If these are touched with water, after the animal has had its fill of water, no reaction occurs. If, however, they are touched with sugar-water, sucking starts immediately and there are visible movements of the end of the proboscis and possibly the stylets. If they are touched with salt solutions, the proboscis is withdrawn and the animals regurgitate. It thus seems certain that the tip of the proboscis bears contact chemoreceptors. Other receptors may be present, and thus the organs described by Weber (1928), Elson (1937), and MacGill (1947) on the epipharynx or wall of the pharynx may be gustatory. Weber's (1933) statement, however, that the sense-organs at the tip of the proboscis of bugs are not taste-organs is incorrect, at least so far as *Oncopeltus fasciatus* is concerned.

Pieris rapae, Imported Cabbageworm Butterflies.—The insects were mounted by clipping the wings together with spring clothes-pins, and were tested only by dipping the tarsi and proboscis in watch-glasses containing water and sucrose solution. Operations were performed to locate the segments of the tarsi involved. The receptors were thus found to be on all the tarsal segments of the fore tarsi, on the middle tarsi, probably at the same places, and at the tip of the proboscis. The reactions of this animal to water-vapor complicate the testing greatly. As noted by Minnich (1929b) and Anderson (1932), this butterfly is difficult to bring to zero response to water and is not always consistent in reactions. With this word of caution, the following seem to bear no receptors: the antennae, parts of the legs other than the tarsi, and the tarsi of the hind legs. The results with the hind tarsi were quite spotty; occasionally the insects seemed to give a little evidence of reception, when the fore and middle legs were removed, but more often not. The occasional positives could have been caused by accidentally touching the proboscis to the solution in the watch-glass. In some cases, also, the animals drank water, after giving what seemed a positive response to sucrose solution, and were later entirely negative to the solution. The situation with respect to the hind legs, therefore, needs further clarification.

Colias philodice, Clouded Sulfur Butterfly.—The results were almost identical with those in *P. rapae*. The tarsi of the fore and middle legs and tip of the proboscis bear contact chemoreceptors, the antennae not. This species, as *P. rapae*, is difficult to work with, because of the irregular responses to water and water-vapor.

Danaus plexippus, Monarch Butterflies.—The *larvae* were tested by fasten-

ing them dorsal side down on wax blocks, holding the animals in place with strings fastened in the wax. All the experiments were done by local stimulation. The criterion used for reception was, as in the experiments of Dethier (1937), feeding movements to sucrose solution, following neutral responses to water. Unfortunately, the insects have the habit of moving the mouth-parts at all sort of provocations—touching, applying water, etc. The experiments indicated, however, that the maxillary palpi, especially the medially directed papillae, and the tip of the hypopharynx bear receptors. Results with the epipharynx and other regions were unsatisfactory, because of the movements noted above. An interesting observation was made with the tarsi. If these were moistened with water, the insects gave no indication of a response to this, but, if moistened with sucrose solution, the tarsi were brought to the mouth-parts and the material removed. Does this mean that the tarsi of the caterpillars of this form bear contact chemoreceptors? Our experiments so far do not allow us to answer this unequivocally either way. The larvae of Lepidoptera are, of course, mandibulate, and the present results and those of Dethier (1937) are fully concordant with the results obtained with other mandibulate forms. The palpi, and hypopharynx bear gustatory end-organs, and the epipharynx (Dethier, 1937) probably does also.

The *adults* were tested with all the methods used with *P. americana*, except determination of thresholds, and with the addition of gross stimulation of the tarsi with solutions in watch-glasses. The results were quite clear-cut, since the reactions of this butterfly are clear and unmistakable, and the water response is easy to control. In tests for receptors on the proboscis the tarsi were either removed or the legs were held against the bodies of the insects by strips of paper fastened in the wax blocks. All the individuals used in these tests were reared from larvae collected in the field, and were mounted, the day after emergence from the pupa, by fastening the wings together with spring clothes-pins.

The antennae, palpi, and rudimentary fore-legs do not bear gustatory receptors. Segments 2 to 5 and the distal end of segment 1 of the tarsi of the middle and hind legs bear receptors. All other parts of the legs do not. The proboscis bears receptors at the tip and for at least 20 mm. back. With the terminal 20 mm. of the proboscis removed the animals cannot distinguish sugar-water from distilled water, but they do not take salt solutions. This may, however, be due to stimulation by the salts of the cut ends of nerves. At least, the terminal portion of the proboscis bears these receptors, and others may be present either on the proboscis or in the mouth itself.

The present experiments add one new species of butterfly, *C. philodice*, to the list of those known to have tarsal receptors and check previous work of Minnich (1921, 1922a and b) and Anderson (1932) on two others. It would seem, therefore, that tarsal chemoreceptors are widely distributed in the butterflies, but so far only negative findings have been reported for moths (Weis, 1930).

Eristalis sp., Drone Fly.—Using local stimulation and extirpation methods,

the end-organs were found to be on the labella and on the tarsi of all the legs, the fore tarsi seeming most sensitive. The labellar receptors are relatively short hairs at the margins, particularly at the anterior end of the labella. At the posterior angle of the labella there are also long hairs present, but these seem to be only tactile. Touching them with a dry grass needle, or one moistened with distilled water, causes only a rippling movement of the labella, and touching them with a needle moistened with sugar-water causes no different response. With the anteriorly located, shorter hairs, touching with a glass needle with sucrose solution brings about an immediate proboscis response. The antennae and palpi seem to lack gustatory receptors.

Phormia regina, Black Blow Fly.—The experiments were similar to those already discussed at length in the paper on the horse fly (Frings and O'Neal, 1946), consisting of local stimulation and extirpation tests. The tarsi and possibly the distal ends of the tibiae of the fore, middle, and hind legs bear receptors. All other parts of the legs lack them. The labella also have receptors, and local stimulation experiments showed these to be the slightly curved shorter hairs lying among the longer tactile hairs.

Since this conclusion differs from that of Minnich (1926b) with the same species, it might be worthwhile to suggest a possible explanation. Minnich used fine brushes in his work, and with these he touched individual hairs, that is the long hairs at the margins. It is our experience that, unless a brush is trimmed until the point consists of single hair (and that would have to be extremely fine), it is impossible to touch just one of the tactile hairs without concomitantly touching one of the shorter hairs as well. With a fine glass needle, it is possible to bend an individual tactile hair and thus to note that, when the needle is moistened with sugar solution, the reaction obtained is the same as that obtained with a dry needle. Reaching in nearer the proboscis with the needle, however, so as to touch the shorter hairs, brings about an immediate response. The experiments are complicated by occasional responses on the part of some of the flies to contact alone, especially if very hungry, and by the limits of stability of the human hand when working under a microscope. It seems, therefore, that Minnich, in his work, may have unwittingly touched the shorter hairs lying so thickly among the longer ones, and thus obtained the responses he reports.

The antennae and palpi apparently do not bear contact chemoreceptors. In fact, removal of the tarsi and terminal portions of the tibiae of all the legs with the labella, so far as could be told by these experiments, rendered the insects unable to taste. Insects thus treated accepted water, sugar-water, and salt solutions indiscriminately. The tarsi and labella, therefore, may be the sole loci of contact chemoreceptors in this species.

Phaenicia sericata, Green-bottle Fly.—The results were similar to those for *P. regina*, as might be expected, but not so complete a series of experiments was performed. The tarsi of the legs and the labella bear the end-organs, while the antennae do not.

Musca domestica, House Fly.—The experiments with this species were rather complete, involving both local stimulation and removal of parts. The four terminal segments of the tarsi of the legs bear contact chemoreceptors. The shorter hairs on the labella are contact chemoreceptors, while the longer ones seem to be tactile, as in *P. regina.* The hairs on the labella of this species seem even more clearly visible than those of *P. regina,* and thus the results were very distinct. The antennae and palpi do not bear receptors. Thus the statements by Wesché (1904) and Lowne (1870, 1890) that the palpi bear taste-organs are incorrect so far as can be determined now. These experiments fully check the work of Deonier (1938, 1939c) and Deonier and Richardson (1935) on this species.

Thus, for the Diptera, these experiments add one new species, *Eristalis* sp., to those already known to have tarsal receptors and check the previous work on two other species. They further show that hairs, usually not the longest hairs, on the labella are the gustatory end-organs. The tarsal organs and these hairs on the labella, with the possibility that the interpseudotracheal papillae may be active, may be the only contact chemoreceptors in the flies tested so far.

Polistes sp., Polistes Wasp.—The "proboscis response" used as an index of reception is quite distinctive, consisting of extension of the labium. The palpal tips, the fore tarsi and the antennae bear receptors. The middle and hind tarsi seem relatively insensitive, and may lack receptors entirely. Receptors on the antennae are located on all the segments except possibly the basal one (scape). The tip of the labium (glossae and paraglossae) also bears receptors, and there are probably others, but these have so far not been located.

Vespula maculata, Bald-Faced Hornet.—Only an incomplete series of tests was made with this species. The palpi definitely have end-organs on their tips. The antennae and tarsi, however, seem not to bear receptors, but the evidence is inconclusive. Kunze (1933) found the antennae of both *Vespa* and *Polistes* bearing receptors. This study confirms that fact for *Polistes,* but possibly not for *Vespa.* Our results, however, for the latter were not conclusive.

Apis mellifera, Honey Bee.—The experiments with this animal were like those performed on other haustellate types. The tarsi of the fore legs bear receptors, as Minnich (1932) and Marshall (1935a) found. The 8 terminal segments of the antennae also have receptors, as Kunze (1933) discovered. The tarsi of the middle and hind legs do not seem to bear contact chemoreceptors. When the fore tarsi are removed and care is taken to avoid touching the antennae with the needles or brushes used to touch the middle and hind tarsi, no responses are obtained. With the thought in mind that the middle and hind tarsi would be less sensitive than the fore tarsi, solutions of sucrose up to 2 M in strength were used without clear-cut evidence of reception by these parts. Contact chemoreceptors are present on the mouth-parts, probably on the glossa (tongue), but so far these have not been located. Operations on the tongue are difficult, and they interfere critically with the proboscis response which is the index of reception. The labial palpi may or may not bear recep-

TABLE III.—Summary of results of experiments on the location of the contact chemoreceptors in haustellate insects.

Insect	Regions shown to bear contact chemoreceptors	Regions shown probably not to bear contact chemoreceptors
HEMIPTERA		
O. fasciatus	Tarsi of all legs, tip of proboscis	Antennae (?), outside of proboscis except the tip
LEPIDOPTERA		
P. rapae	Tarsal segments 1 to 5 of fore legs, tarsi of middle legs, tip of proboscis	Antennae, tarsi of hind legs (?), other parts of legs than those listed at left
E. philodice	Tarsi of fore legs, tip of proboscis	Antennae
D. plexippus		
Larvae	Tips of maxillary palpi, particularly medial tubercles, ligula	Tarsi (?)
Adults	Segments 2 to 5 and the distal end of segment 1 of middle and hind tarsi, distal 20 mm. of proboscis, possibly other regions in or on proboscis or in mouth	Antennae, palpi, fore legs, all parts of middle and hind legs other than those mentioned at left
DIPTERA		
Eristalis sp.	Tarsi, labella	Antennae, palpi
P. regina	Tarsi and possibly distal ends of tibiae of all legs, labella. These are probably the sole loci of contact chemoreceptors in this species	Antennae, palpi, other segments of legs than those listed at left
P. sericata	Tarsi of all legs, labella	Antennae, palpi
M. domestica	Distal 4 segments of tarsi of all legs, labella	Antennae, palpi, other segments of legs than those listed at left
HYMENOPTERA		
Polistes sp.	Tips of maxillary and labial palpi, fore tarsi, antennae to scapes, glossae and paraglossae of labium	Tarsi of middle and hind legs
V. maculata	Tips of maxillary and labial palpi	Antennae (?), tarsi (?)
A. mellifera	8 terminal segments of antennae, tarsi of fore legs, glossa (?)	Labial palpi (?), tarsi of middle and hind legs

tors. The evidence is inconclusive. Touching the palpi with sugar water usually elicits no response. This might be interpreted as meaning that the labial palpi bear no receptors for taste. The fact that the tip of the proboscis ordinarily is not stimulated previous to proboscis extension, however, suggests that stimulation of the palpi may not be the adequate stimulus for this reflex.

Summary of Results on the Haustellate Orders.—The results of the experiments on the haustellate orders are presented in brief in Table III. In the adults of these orders, tarsal organs are usually present, but antennal receptors seem to be restricted to Hymenoptera. The receptors on the mouth-parts are usually found at or near the tip of the proboscis. In species in which probably all the receptors were located, these receptors were the only ones found.

MORPHOLOGICAL STUDIES

Periplaneta americana.—Photomicrographs of the labium and maxillary palpus are presented in Fig. 1. The regions at the tips of the palpi found to be sensitive in the experimental studies are easily visible. The sensory field on the maxillary palpus, when examined with higher magnification (Fig. 4), can be seen to bear two types of sensilla—a few long trichoid sensilla (about 45 to 55 μ long) and a large number of basiconic sensilla (about 15 μ long). Since the trichoid type is found all along the palpus, but the whole extent of the palpus is not sensitive to chemical stimulation, it seems reasonable to assume that the basiconic sensilla are the end-organs. This is further supported by the fact that, in the sensory patch itself, the basiconic type is by far more numerous. These are very thin-walled and delicate, the entire exoskeleton, as a matter of fact, being quite thin on the whole sensory patch.

Fig. 3.—Ligula of *P. americana* (×200). Note the hair-like exoskeletal covering and the basiconic sensilla, best seen at the tip of the paraglossa at left.

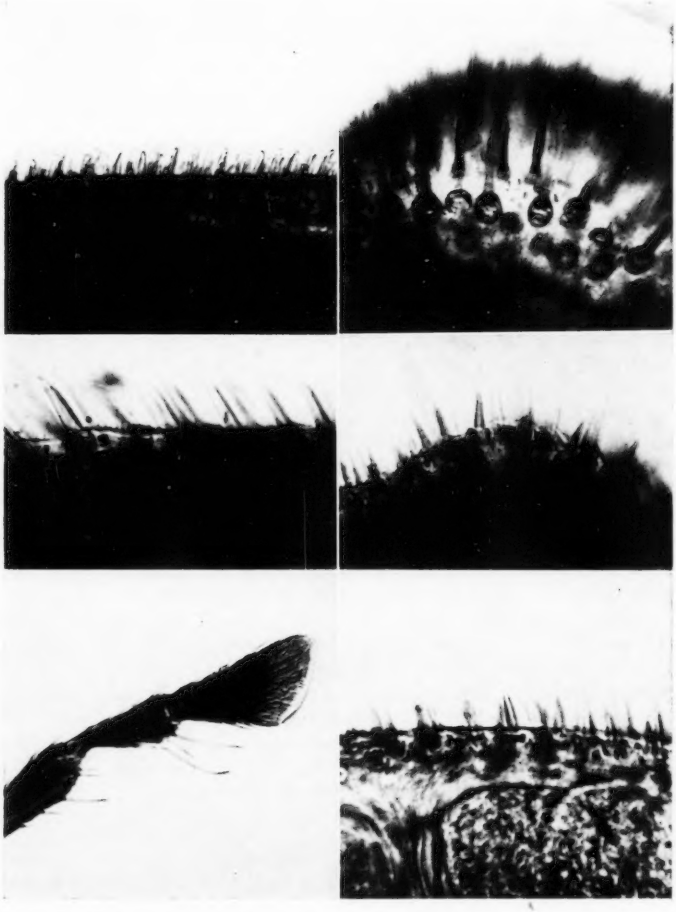

Fig. 4.—(*Above, left*) Sensilla in the sensory field of the maxillary palpus of *P. americana* (×350). (*Above, right*) Sensilla in the sensory field of the tip of the labial palpus of *P. americana* (×350). (*Middle, left*) Sensilla in the sensory field at the tip of the maxillary palpus of *Gryllus assimilis* (×700). (*Middle, right*) Sensilla from the tip of the labial palpus of *Melanoplus differentialis* (×350). (*Below, left*) Maxillary palpus of *Galerita janus* (×30) showing the sensory field at the tip. (*Below, right*) Sensilla from the sensory field of the maxillary palpus of *G. janus* (×700).

The sensory field at the tip of the labial palpus (Fig. 4) bears two types of sensilla also—long trichoid sensilla (about 55 μ long) and shorter trichoid sensilla (about 15 μ long) which are almost basiconic in type. The long trichoid type are the more numerous, and they are much thinner-walled and a little shorter than the other trichoids on the rest of the palpus. It is impossible, at present, to say whether the end-organs involved in contact chemoreception are the long or the short trichoid type, or both. The exoskeleton on the sensory patch seems to be quite thin in this case, as in the case of the maxillary palpus. The delicate nature of the sensory patches on the labial and maxillary palpi is clearly shown by the fact that, in the preparation of whole mounts with Diaphane, these may be drawn inward to form concave invaginations, if the specimens are placed in high concentrations of alcohol without first being brought through gradual intermediate steps.

On the ligula of the labium (Fig. 3) there are patches of a hairlike outgrowth of the exoskeleton. These "hairs" do not seem to be sensilla. Mixed with this mass of "hair," however, are two kinds of sensilla—trichoid sensilla (about 140-175 μ long), like those found widely distributed over the mouthparts, and sensilla resembling those found on the tips of the labial palpi which could be called either short trichoid or long basiconic sensilla (about 20-25 μ long). Since the latter are restricted to the regions shown by this study to be sensitive to chemicals—i.e., the tips of the glossae and paraglossae—it is probable that they are the end-organs.

The tip of the hypopharynx is clothed with a mass of "hairs" exactly like those found on the ligula, but there seem to be no sensilla present. Trichoid, coeloconic, and basiconic sensilla are found along the lateral edges. Either one or both of the latter two types are possibly the end-organs.

It seems probable, therefore, that the receptors are the basiconic sensilla, which may be long enough to resemble short trichoid types, found in the regions shown to be chemoreceptive experimentally. This view is further supported by the fact that regions of the mouth-parts other than those shown to be sensitive do not bear these organs, nor do the legs or antennae. The possibility remains that the thin-walled trichoid sensilla of the labial palpi and the coeloconic or trichoid sensilla on the hypopharynx may also serve as contact chemoreceptors.

Blattella germanica.—The appearance and distribution of sensilla on the mouth-parts of this species are almost exactly the same as in the preceding species. The organs are about the same size, though the mouth-parts, as a whole, are smaller.

Gryllus assimilis.—The sensitive regions on the tips of the palpi are clearly delimited in this species. The tips of the maxillary palpi, instead of the sides as in the roaches, bear the sensory fields. The organs found on the fields of the maxillary palpi are all of one type—basiconic sensilla (about 18 μ long) with thin walls and well developed bases (Fig. 4). Since there are no other types of sensilla present within the sensory field, it is almost certain that the basiconic sensilla are the end-organs. On the tips of the labial palpi there are

two types of sensilla—long trichoid (about 75 μ long) and short trichoid types (about 25 μ long). Since the shorter type is thinner-walled and more like the sensilla on the maxillary palpus, it is reasonable to assume that these are the end-organs on the labial palpus, but there is no direct evidence for this.

Melanoplus differentialis.—The maxillary and labial palpi of the grasshopper bear sensory fields at the tips. The only sensilla present on both the maxillary and labial palpal tips (Fig. 4) are the peg-like basiconic type (about 20 μ long). It is thus almost certain that this is the type involved in contact chemoreception. Since no sensilla other than a heavy trichoid type are present on the ligula and since the ligula has been shown not to bear receptors, the belief that the basiconic sensilla are the end-organs is given further substantiation. Other regions of the mouth-parts have not been studied so far.

Tenodera a. sinensis.—The tips of the palpi bear only trichoid sensilla. These are distinguishable from the ordinary trichoid type found all over the palpi by being rather shorter (long type about 100-105 μ long, shorter type about 30 μ long on the maxillary palpus and about 70 μ long on the labial palpus). They also appear thinner walled, but they cannot, by any stretching of the term, be called basiconic. There are only five or six of the shorter type on each palpus; indeed, the palpi bear relatively few sensilla of any kind. A few of the shorter trichoid type, resembling those on the palpal tips, are found also on the paraglossae and glossae, and these may be receptors on those parts, but experimental proof is lacking.

Thermobia domestica.—The maxillary palpi (Fig. 2) bear only trichoid sensilla, which are seemingly the same all along their extent. The maxillary palpi, however, were found not to bear contact chemoreceptors. The tips of the labial palpi, which were found to be chemoreceptive, bear numerous thin-walled trichoid sensilla of various lengths, and a group of five tuft-like structures, the nature of which we have not determined. So far, these morphological studies have not given any clue as to the nature of the end-organs involved.

Chrysopa sp.—The basiconic sensilla in sensory patches on the tips of the maxillary and labial palpi are quite small (about 5 μ long over all), but quite definitely visible. There are also present on the palpi longer trichoid sensilla (about 65 to 75 μ long), but these are wide-spread over the palpi and other regions of the mouth-parts. It seems probable that the small basiconic sensilla, restricted to the sensory patches at the tips, are the palpal receptors involved.

Libellula sp.—Since the experiments did not enable us to determine the loci of the end-organs, if any, involved in contact chemoreception, morphological studies would be without experimental roots, and none are reported.

Galerita janus.—The maxillary palpus and the organs found on the sensory patch at its tip are shown in Fig. 4. These basiconic sensilla are about 10 μ long from the base to the tip. Since no other sensilla are present on the

sensory patch, it is certain that these are the contact chemoreceptors. Studies of other regions of the mouth-parts have not so far been made.

Epicauta pennsylvanica.—On the tips of the maxillary and labial palpi are well-defined sensory fields containing only basiconic sensilla (about 10-12 μ long), which, therefore, are probably the contact chemoreceptors. These are quite like those of *G. janus* in appearance, and thus no photomicrograph is presented. Since the other loci of receptors on the mouth-parts were not determined, no further morphological studies are reported.

Chauliognathus pennsylvanicus.—The maxillary palpus has a sensory patch along the inner edge of the tip. The labial palpus has a distinct patch at the outer edge. In each case, the only type of sensillum in the patch is a basiconic type (about 15 μ long on the maxillary palpus and about 25 μ long on the labial palpus). Around the patches are longer trichoid sensilla and these extend all over the palpus. It seems reasonable, therefore, to assume that the basiconic type is the contact chemoreceptor in this form. This type of sensillum, found for *G. janus, E. pennsylvanica,* and *C. pennsylvanicus,* is the same morphologically as those found on the palpal tips by the German workers on beetles and by Valentine (1931). Crombie (1944) and McIndoo (1929) described similar organs from the palpal tips of *Rhizopertha* and *Epilachna,* and these are probably contact chemoreceptors in these forms.

Tetraopes tetraophthalmus.—We have so far made no morphologic studies on this form.

Oncopeltus fasciatus.—At the tip of the proboscis there is a small field of peg-like organs, each about 10 μ long, and a few delicate thin-walled trichoid sensilla, about 25 μ long. There are also present two long trichoid sensilla, about 75 μ long. The smaller trichoid type is found all along the proboscis,

Fig. 5.—Terminal segments of the fore tarsus of *Pieris rapae* (×100). The fine trichoid sensilla on the ventral side may be contact chemoreceptors.

and thus may probably be eliminated as the chemoreceptor, since the tip of the proboscis alone seems to bear the receptors. This leaves the two long trichoid sensilla and the field of basiconic sensilla as possibilities. The resemblance of the long trichoid type to hairs spread widely over the bodies of the insects, suggests that the true chemoreceptors are the basiconic sensilla, but direct proof is lacking. On the tarsi there are many types of sensilla, and we are unable, at present, to assign a gustatory function to any one of these.

Pieris rapae.—On the proboscis of this form there are two types of sensilla —short, thin, trichoid sensilla (about 8 μ long) distributed all along the outside of the proboscis and also found on the inner surface of the proboscis, and very short, blunt, thin-walled pegs in pits (extending about 4 μ above the surface), restricted to the outside of the proboscis near the tip, especially numerous at the tip. Which if these may be the contact chemoreceptors, we are not prepared to say.

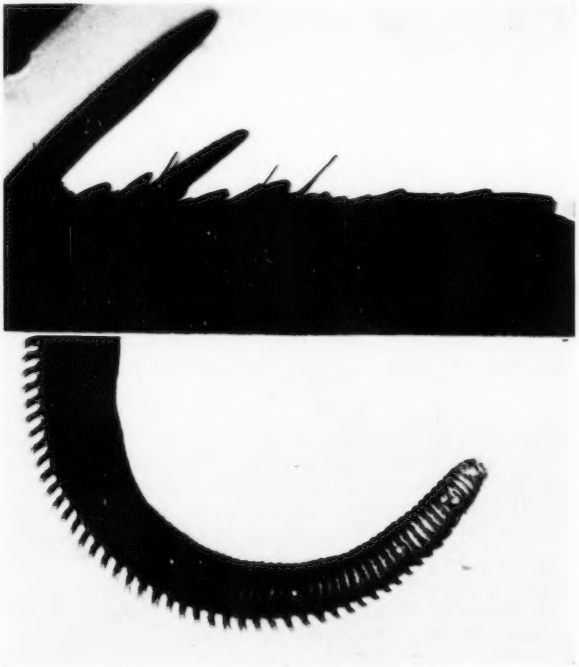

Fig. 6.—(*Above*) Portion of the ventral surface of the terminal segment of the middle tarsus of *Danaus plexippus* (×100). The thin-walled trichoid sensilla found among the scales and long spines may be chemoreceptive. (*Below*) Tip of the proboscis of *D. plexippus* (×100) showing the pit-peg (coeloconic) organs.

On the tarsi of the fore and middle legs, along with heavy spines and long trichoid sensilla, are shorter thin-walled sensilla, about 40 μ long (Fig. 5) These are on the ventral sides of the tarsi on all the segments. They are present also on the hind tarsi, but very sparsely scattered, not in groups as on the fore and middle tarsi. While there is no direct evidence that these are the tarsal receptors, they are admirably suited in position and structure to be the tarsal receptors experimentally demonstrated in this form.

Colias philodice.—We have prepared no slides of this form, and consequently report no morphological studies.

Danaus plexippus.—No studies have been made of the larval parts. On the proboscis of the adult, there are present the two types of sensilla described above for *P. rapae*, but the trichoid sensilla are far fewer. The peg-like organs in pits on the outside of the proboscis (Fig. 6), extend about 7 μ above the surface. The tiny hairs extend about 8μ above the surface. The pit pegs are present only at the tip and for about 400 μ back on the outside of the proboscis. The tiny hairs are not found at the tip, the first one which could be found on the outside being about 175 μ back from the tip. Inside the proboscis there are trichoid sensilla like those outside, but a little longer. The internal hairs are found in a neat line on the lateral walls about 100 μ apart. Which of these organs may be the end-organs, it is impossible to say at present, but the fact that removal of the terminal 20 mm. of the proboscis did not destroy the ability to taste, makes it seem probable that the trichoid type is the receptor. Whether both the sensilla inside the proboscis and those outside are involved or not, these experiments do not allow us to decide.

The tarsi are heavily clothed with scales and spines, and this renders a study of them difficult. There are present among the heavy spines and scales, however, thin clear hairs about 85 μ long, which are found on all the segments of the tarsi, but not elsewhere on the legs. These are shown in Fig. 6. It is possible that these may be the receptors involved in tarsal reception in this form.

Eristalis sp.—On the front edge of the labella there are trichoid sensilla of three lengths which are not clearly separable (Fig. 7). One type averages about 55 to 70 μ long, the second about 35 to 40 μ long and the third about 18 μ long. There is present also a pelage-like outgrowth of the exoskeleton, about 4 μ thick. At the rear of the labella, the long hairs are longer than at the front (about 85 to 100 μ long), and long tactile hairs (about 175 μ long) are also present. Between the pseudotracheae are the interpseudotracheal papillae. Since the labella were stimulated when the inner surfaces were pressed together and therefore the interpseudotracheal papillae were not exposed, it is obvious that one or more of the trichoid sensilla described above are contact chemoreceptors, but further differentiation is not possible at present. The tarsi are heavily clothed with trichoid sensilla and spines. We have not succeeded so far in seeing single sensilla clearly enough to postulate any possible receptors on the tarsi.

Phormia regina.—The labella closely resemble the labella of *M. domestica*, shown in Fig. 8. The long hairs were shown experimentally to be tactile. Near the anterior tip they are about 180 μ long, and near the posterior tip about 300 μ long. The shorter hairs, about 70-80 μ long, were found to be contact chemoreceptors. There are no other sensilla present in the regions found by local stimulation to be receptive of contact chemical stimuli. On the upper surface of the labella there are very small hairs (about 15 μ long) in small groups, but their location rules them out as having been touched by the needles in our experiments. The "pelage" on the labella is about 7 μ deep and cleary visible. It is the presence of this presumably non-sensory "pelage" that gave rise to the use of the term, "medium sized hairs" in the previous report on *Tabanus* (Frings and O'Neal, 1946). The interpseudotracheal papillae are about 10 μ high. Since the labella are kept closed when at rest, the interpseudotracheal papillae were not touched by the needles used in the experiments. There is no evidence from this study that these may not be contact chemoreceptors, but at least the shorter trichoid sensilla at the rim of the

Fig. 7.—(*Above*) Anterior tip of the labella of *Eristalis* sp. (×400). (*Below*) Anterior tip of the labella of *Musca domestica* (×400).

labella are definitely such receptors. Since the blow fly possesses olfactory receptors on the labella (Frings, 1941) and since the long trichoid type have been shown to be tactile in this study while the shorter ones are contact chemoreceptors, it may not be amiss to suggest that the interpseudotracheal papillae may be the distance chemoreceptors.

We have not succeeded so far in finding possible receptors on the tarsi of blow flies.

Phaenicia sericata.—No studies have been made on the end-organs on the labella and tarsi of this species.

Musca domestica.—The expanded labella of this species are shown in Fig. 8. The long trichoid sensilla (about 180-200 μ long at the anterior margin and about 300 μ long behind) shown to be tactile are clearly visible, and lying among them the shorter trichoids (about 45-60 μ long) which are contact chemoreceptors. The only other possible receptors on the labella are the interpseudotracheal papillae. The surface of the exoskeleton is covered with the pelage-like outgrowth found in the other species of flies, about 7 μ deep in this species. As suggested for *P. regina*, the interpseudotracheal papillae may not be gustatory receptors at all, but possibly olfactory, though both direct and

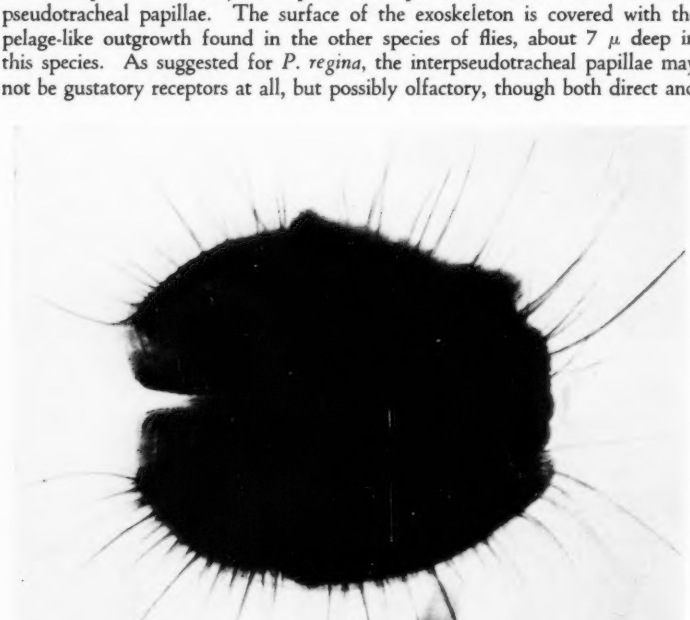

Fig. 8.—Labella of *Musca domestica* (×80). The long trichoid sensilla were found to be tactile, the shorter trichoid sensilla are contact chemoreceptors.

TABLE IV.—The loci of contact chemoreceptors in the insects used in this study. Mandibulate forms are listed in the upper half of the table and haustellate forms are in the lower half. (+ = receptors present on part listed in heading; — = receptors not present; no entry means that the part was not tested, or that the results were not clear-cut, or that the part is not present in the species listed).

Insect	Labial tip	Tips of labial palpi	Maxillary tips	Tips of maxillary palpi	Hypopharynx	Fore tarsi	Middle tarsi	Hind tarsi	Antennae
T. domestica	+	+	—	—		—	—	—	—
P. americana	+	+	—	+	+	—	—	—	—
B. germanica	+	+	—	+	+	—	—	—	—
G. assimilis		+		+		—	—	—	—
M. differentialis	—	+	—	+	+	—	—	—	—
T. sinensis		+		+		—	—	—	—
Chrysopa sp.		+		+		—	—	—	—
Libellula sp.						—	—	—	—
G. janus	+	+		+		—	—	—	—
E. pennsylvanica	+	+		+		—	—	—	—
C. pennsylvanicus		+	—	+		—	—	—	—
T. tetraophthalmus	+	+		+		—	—	—	—
D. plexippus (larva)	+			+					
O. fasciatus	+		+			+	+	+	— (?)
P. rapae		—	+			+	+	— (?)	—
C. philodice			+			+			—
D. plexippus (adult)		—	+			—	+	+	—
Eristalis sp.		+ (labella)		—		+	+	+	—
P. regina		+ (labella)		—		+	+	+	—
P. sericata		+ (labella)		—		+	+	+	—
M. domestica		+ (labella)		—		+	+	+	—
Polistes sp.	+	+		+		+	—	—	+
V. maculata		+		+		— (?)	— (?)	— (?)	— (?)
A. mellifera	+ (?)	— (?)				+	—	—	+

indirect proof is lacking for this species. The tarsi have been studied histologically by Hayes and Liu (1947), and the thin-walled hairs found by them on the terminal four segments are easily seen in whole mounts. These thin-walled hairs are replaced on the basal segment by heavy spines, correlating well with the lack of receptive capacity on the basal segment.

Polistes sp.—A photomicrograph of the labium of this species is presented in Fig. 9. This shows the organs on the tips of the labial palpi, glossae and paraglossae which are possibly the contact chemoreceptors, since these points were shown experimentally to be the loci of the end-organs. They are trichoid in type, curved at the tips, about 40 μ long on the labial palpi and the glossae and about 50 μ long on the paraglossae. Sensilla exactly like these are found on the tips of the maxillary palpi also and are there about 35 μ long. That these are the actual end-organs seems probable, since they are characteristic in size and shape, as against other trichoid sensilla on the mouth-parts, and found on the spots shown to be receptive experimentally. The tarsi and antennae bear a confusing array of possible end-organs, and it is impossible at present to decide which ones might be the actual contact chemoreceptors.

Vespula maculata.—So far no morphological studies on this form have been made.

Apis mellifera.—To return to a discussion of the possible end-organs on the eight terminal segments of the antenna of this species would be, as Forel

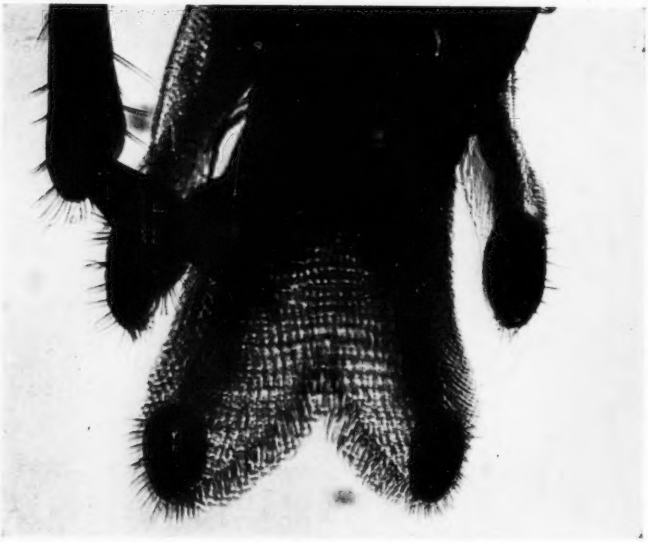

Fig. 9.—Ligula and labial palpi of *Polistes*. (×100).

(1900) says about the sense of smell in insects, "gilding refined gold." These possibilities have been discussed thoroughly by Frisch (1921), Minnich (1932), and by many workers on the morphology of the antennae of *Apis*. Since our experiments do not allow us to designate any particular end-organ as the one involved, we shall essay no discussion of possibilities. The fore tarsi are clothed with hairs of more than one type; which would be the receptors we are unable to say. Since the experiments did not determine the exact loci of the gustatory organs on the mouth-parts, no detailed description of these parts is presented.

Summary of Morphological Studies.—From these studies it seems obvious that the actual end-organs on the palpal tips of the mandibulate insects are basiconic sensilla, often being long enough, however, to be classed possibly as short trichoid sensilla. The sensilla on other regions of the mouth-parts may be either basiconic, trichoid, or coeloconic. Where accurately determined, as for the palpi of the roach, cricket and grasshopper, the basiconic sensilla are definitely contact chemoreceptors. This checks well with the discoveries of previous workers on beetles.

In the haustellate orders, on the other hand, the sensilla which have been shown to be the actual end-organs for contact chemoreception are definitely trichoid. These trichoid sensilla, however, are often blunt rather than pointed, and thus give some indication of having possibly been derived from a basiconic ancestral type (cf. for instance, *Oncopeltus* and *Eristalis*).

For all insects there is need for much further experimental work to determine exactly the loci of contact chemoreceptors, so that morphological studies can be interpreted unequivocally.

DISCUSSION

To give some general over-all picture of the loci of contact chemoreceptors in the orders of insects studied herein, Table IV is presented. From this it is obvious that the most constant loci for contact chemoreceptors in all forms are the tips of the labial palpi (assuming that the labella of the Diptera actually correspond to the labial palpi). The only group in which labial palpi are present without these receptors is the Lepidoptera. The maxillary palpi, where present, also are apt to bear contact chemoreceptors. The only groups in which they were found lacking were the Thysanura and Diptera. The ligula, also, and the hypopharynx, where present, are likely to bear these receptors. Tarsal receptors are restricted to the haustellate orders, even possibly to haustellate stages in the life cycle of insects with mandibulate larvae, such as the Lepidoptera, or to haustellate species in orders which have both haustellate and mandibulate types, such as the Hymenoptera. Antennal receptors have been found so far only in some of the Hymenoptera, thus being quite restricted in distribution.

It is worth noting that the paper by Dethier (1947) was published after these experiments were completed, and therefore the presence or absence of contact chemoreceptors on the ovipositor was not tested for. Actually the

receptors located by our experiments are those involved in feeding reactions. It is certainly possible that contact chemoreceptors, resembling perhaps the common chemical receptors of Vertebrates, may be found on other parts of the bodies of insects.

It is interesting to note, from Table IV, that the insects which have tarsal and antennal receptors are those whose habits are such as to "require" them, as Nagel (1894) postulated. Thus predaceous, omnivorous, and phytophageous mandibulate forms lack these, while the flower-frequenting haustellate types have them. It would seem that Minnich's (1932) suggestion that the ancestral insect had contact chemoreceptors distributed widely on all the appendages may not be true. The ancestral insect was probably mandibulate. While it is, of course, impossible to state with certainty the distribution of the contact chemoreceptors in this insect type, it is reasonable to assume that the distribution would probably be most like that of recent thysanuroid or orthopteroid insects. This would mean that the contact chemoreceptors, with the possible exception of those on the ovipositor, would be found on the palpi and other regions of the mouth-parts. The occurrence of these receptors on the antennae and tarsi of the higher insects would, therefore, seem to be a case of secondary specialization.

The claim of McIndoo (1934) that tarsal chemoreception was really tarsal tacto-olfaction has already been discussed. There is really an important point at issue here. Are the distance and contact chemical senses of insects really separate? A complete discussion of this matter would lead us too far afield from the present matter, and will not be attempted. Marshall (1935b) stated that it is possible that insects have only chemoreceptors, and that these are of different sensitivities, those on the antennae being most sensitive and therefore usually acting as distance receptors, those on the mouth-parts being less sensitive and usually acting as contact receptors but sometimes as distance chemoreceptors, and those on the tarsi being least sensitive and acting only as contact receptors. The present state of our knowledge of chemosensitivity of insects does not allow us to decide this issue definitely. It may be, thus, that contact chemoreceptors, as defined in this paper, tested for by the use of compounds non-odorous to man, may be only one type in a galaxy of general chemoreceptors on the insect body. This method of testing, however, at least enables us to find chemoreceptors which have the common property of being stimulated by non-volatile, water-soluble substances which in higher animals stimulate gustatory receptors. The experiments of Frisch (1934), Schaller (1926), Ritter (1936), and Bauer (1938) on various insects, however, showing that they can distinguish the different modalities of taste by means of the receptors on the mouth-parts, strengthens our belief that the receptors thus discovered are true gustatory receptors.[5]

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5 It will be noted that, throughout this paper, the terms, gustatory, taste, contact chemoreceptive, and tactochemical, have been used synonymously. With the present state of our knowledge in this field, these terms, if used without perceptual implications, are impossible to separate.

From the morphological studies, it is obvious that there is no such thing as an anatomically differentiatable contact chemoreceptor. Two types of sensilla have been shown to be contact chemoreceptors—basiconic and trichoid—and there has been shown to be a loose relationship between the type of receptor and the feeding habits of insects, whatever this may mean. But this separation is not clear-cut, and with the further possibility that other types of sensilla may also be involved, it is clear that anatomical studies are not sufficient to prove that a particular sensillum is a contact chemoreceptor, unless backed up by critical experiments.

It may be that it will be possible, with histological methods, to distinguish between chemoreceptive and non-chemoreceptive sensilla by the absence or presence of a terminal strand or a group of basal nerve-cells (Snodgrass, 1935). It is now possible for histological studies to be made of organs shown definitely to be contact chemoreceptors—the pegs on the palpi of the grasshopper or cricket, for instance, or the hairs on the labella of the house fly or blow fly. These studies, backed up by experimental demonstrations of the functions of the sensilla, may enable histologists to determine the true structure of a contact chemoreceptor and thus make possible histological identification with some certainty.

Finally, as pointed out earlier, these experiments must be considered as only a beginning. They should indicate the future course which will give us information as to the location and nature of the contact chemoreceptors of insects. First, there must be experimental determination of the loci of the receptors and, where possible, of the exact end-organs. Then there can follow morphological and histological studies. Such combined work should yield the raw data from which fruitful generalizations concerning the location and nature of these receptors in insects can be formulated.

SUMMARY

A review of the published work on the location of the contact chemoreceptors of insects reveals that these have been found on the mouth-parts (particularly the palpi of mandibulate insects and the labella of flies), the tarsi of butterflies, flies and bees, the antennae of bees, and the ovipositors of a few hymenopterous parasites. The actual end-organs on these parts are in most cases unknown, but may be thin-walled basiconic, coeloconic or trichoid sensilla. In view of the many parts of the body which may bear these receptors and the differences in form of the suspected end-organs, morphological studies based on criteria of location or structure, without experimental support, are of little value.

In the present work, 23 species from the orders, Thysanura, Orthoptera, Neuroptera, Odonata, Coleoptera, Hemiptera, Lepidoptera, Diptera and Hymenoptera were studied. The insects were mounted alive on wax blocks for exact observations, though some tests were also made with free animals. The loci of contact chemoreceptors were found by: 1. local stimulation experiments, in which particular organs or even sensilla were touched with fine

needles bearing sapid solutions, following control tests, and 2. extirpation experiments, in which organs were removed and the reactions of the animals to sapid solutions before and after the removal were observed. Nutritional and water controls were provided in all experiments.

In the mandibulate insects, where loci could be determined accurately, the tips of the maxillary palpi (except for possibly the firebrat) and the labial palpi were found to bear contact chemoreceptors. The probable end-organs are either basiconic or trichoid in shape and usually found in definite sensory fields. Other receptors were found to be present on the mouth-parts in the insects tested. In two species of roaches, they were located on the hypopharynx and the tip of the labium (ligula). In one species of grasshopper, they were found only on the hypopharynx. In these three species there was no evidence that receptors existed at other places on the mouth-parts or in the mouth or pharynx. The antennae, tarsi, and cerci, where present, of mandibulate insects seem not to bear contact chemoreceptors.

In the haustellate insects, tarsal chemoreceptors are present in many species. These may be only on the fore tarsi, as in the honey bee, or on all the tarsi, as in the house fly. They are generally on the four terminal tarsal segments and, in some species, on the proximal tarsal segment and even possibly the distal end of the tibia. Where the sensilla were located, they were found to be thin-walled and trichoid in type. Antennal receptors were found only in the honey bee and the *Polistes* wasp, of the species tested. In the bee, they are on the eight terminal segments of the antenna, and in the wasp on all segments except the basal one. The antennal end-organs were not determined. The receptors on the mouth-parts of haustellate insects are usually at or near the tip of the proboscis. These were located accurately in certain Diptera, and were found to be trichoid in type. In the species of Diptera where all the end-organs were probably located, the tarsal and labellar receptors were the only ones found.

Neither the experimental nor the morphological studies made so far allow unequivocal generalizations with respect to either position or structure of the contact chemoreceptors of insects. Differences in the loci and appearance have been found even in insects from the same order, such as the roach and the grasshopper. The differences among insects in the distribution and structure of contact chemoreceptors seem to be related to food habits, but the relationships are obscure at present. Much further experimental work is necessary, followed by morphological and histological studies of organs shown experimentally to be contact chemoreceptors, before fruitful generalizations will be possible.

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An Experiment on Peromyscus Homing

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The homing ability of small mammals has been demonstrated by several workers. The factors that affect this ability are unknown and there is no generally accepted explanation of the behavior. Chitty (1937) suggested that returns over shorter distances might be explained by the mice having larger ranges than expected. He thought also that returns over greater distances might be the result of random wandering bringing the animals into a familiar area.

Other workers believed the distances were too great and the percentages of returns too high to be explained by random wandering (See especially Burt 1940, Fenyuk and Sheikina 1938). Kendeigh (1944) believed that the homing mice he observed must have been familiar with the terrain over an area wider than their usual home range.

TABLE I.—Homing of *Peromyscus*.
(Compiled from Murie and Murie 1931)

Distance Transferred	Number Transferred	Number Homed
100 to 1100 yards	34	29
0.7 mile	8	1
1+ miles	49	6*
2 miles	23	1
4 miles	15	0

* One of these moved 1.5 miles.

Whatever the ability may be, it is apparently weakened with distance. A summary of the work of Murie and Murie (1931) shows this very well (Table I). The mice they were studying (*Peromyscus maniculatus artemisiae*) had a normal cruising range of 100 yards or less.

Homing experiments conducted by Burt (1940) on *Peromyscus leucopus* throw additional light on the problem. These are of particular interest since the work was done in connection with a complete population study where the normal ranges of the mice were determined. The average cruising range of *Peromyscus* reported in these experiments was about 53 yards.

Burt's first trial was made on a 900 by 240 foot strip of woodland, closely set with live traps. Each day for four days the captured mice were released at

the center of the plot. Thirty-seven mice were transferred and 28 (76%) of them traveled 10 to 155 yards to return home.

His second trial was made on a tongue of woodland surrounded by fields on three sides. Mice were transferred greater distances, 160 to 365 yards. Each day mice from the two halves of the experimental plot were moved to the extreme opposite ends. To return home some mice went from east to west and others from west to east. Fifty-one mice were transferred and 17 (33%) returned to their homes.

In the second trial, when the distances were greater, fewer animals homed. However, the greater distances may not have been the only reason for the decreased percentage of homing. It is possible that the presence of mice moving in opposite directions and the availability of vacated ranges in both directions decreased the percentage of returns. On the other hand it is possible that the wanderings of the mice on this tongue of woods were partially restricted

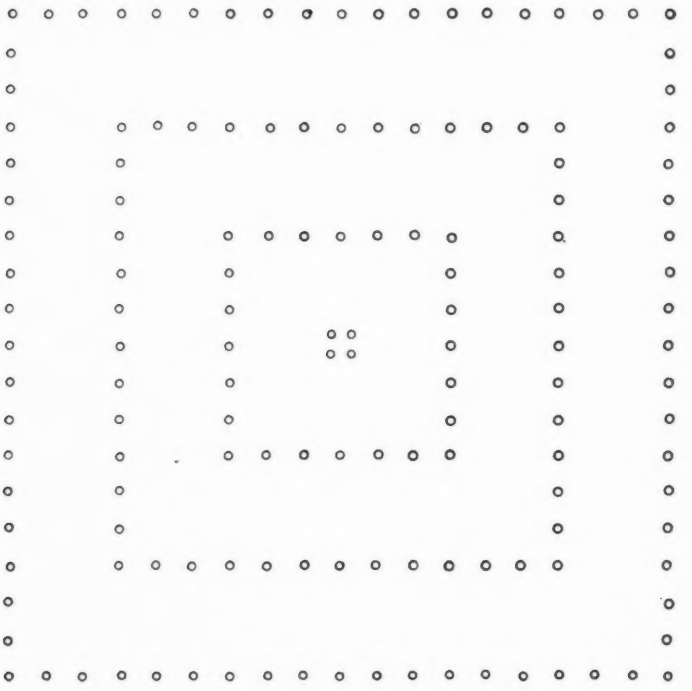

Fig. 1.—Diagram of the trapping plan. Traps were 55 feet apart in the rows, and the concentric squares were 165 feet apart. The entire area comprises 22.5 acres.

by the adjacent fields, so that the mice had a better chance of finding their homes than they would have had within continuous woodland habitat.

Comparing the results of these experiments it seemed possible that the homing behavior was influenced not only by distance but also by the presence of unoccupied ranges, and perhaps by conspicuous habitat variations or landmarks. The homing experiment reported in the present paper was designed to eliminate or reduce these two potential influences. It was planned to bring mice from all directions and release them simultaneously at a central point. The influence of population pressure would then be equalized, with potential home sites available in all directions. The experimental plot was placed in an area of continuous woodland so that the more conspicuous landmarks provided by striking habitat variations would be eliminated .

PROCEDURE

The experimental plot was a 22.5 acre block in the wooded bottomlands of the Patuxent Research Refuge, Maryland. The surrounding habitat was of the same type.

Three concentric, parallel squares were laid out. The sides of the squares were 990, 660, and 330 feet. The distance between adjacent squares was 165 feet. Sherman live traps were set 55 feet apart on the sides of the squares and four traps were set at the center of the inner square. Mice were marked with numbered metal ear tags.

For the first two days, August 27-28, 1946, all mice were released where they were caught. On the third day the mice caught in the traps of the outer square were taken to the center of the plot and released; mice taken in the two inner squares were again released where caught. Trapping was suspended for five days to allow the population to adjust. Trapping was resumed for three days, September 4 through 6.

The distances the mice were transferred when moved from the outer square to the center were 500 to 700 feet depending on whether the trap was at the corner of the square or nearer the middle of one of its sides. These were distances over which a fair percentage of returns were expected on the basis of Burt's studies of the species. The diameter of the average normal range of these mice in the same season and habitat had previously been found to be about 150 feet for males and about 100 feet for females.

RESULTS

Mice transferred.—Fifty-three mice, 29 males and 24 females, were caught in the 72 traps of the outer square on August 29. These were taken to the center of the plot and released. Forty-eight (27 ♂ ♂, 21 ♀ ♀) were adult and subadult animals. Five (2 ♂ ♂, 3 ♀ ♀) were very small juveniles. Similar numbers were taken from each side of the square: 12, 15, 14, and 12.

In the second period, September 4 through 6, 25 of the 27 adult and subadult males and 15 of the 21 females were recaptured. None of the juveniles was retaken. Homing was judged to have occurred if a transported animal was caught in the same or an adjacent trap in both periods. By this criterion,

22 males and 13 females homed. Two additional males and one female may or may not have homed. They were recaptured 110-165 feet from the nearest collection point of the first period. These mice may have been within their home ranges both periods, or they may have taken up residence in slightly different locations from those they had originally occupied (Table II).

TABLE II.—Recapture Records of *Peromyscus*.

Least distance between capture sites in Periods I and II	Animals transferred (adults and subad.)		Animals not transferred (adults and subadults)	
	Males	Females	Males	Females
0	17	10	11	14
55	5	3	4	4
110	1	0	1	1
165	1	1	0	0
173	0	0	2	0
595	0	1	0	0
765	1	0	0	0
Not recaptured	2	6	2	0
Total	27	21	20	19

One male and one female completely failed to home. The female remained near the point of release, 595 feet from her sites of capture the first period. She was trapped each day of both periods. The male was caught in the second period 765 feet from his points of capture the first period. He had traveled in the direction opposite to the one he would have following in homing. He was trapped twice in each period.

To summarize: Of the 27 males transferred (excluding small juveniles) 22 (82%) homed, 2 (7%) possibly homed, 1 (4%) failed to home, and 2 (7%) were not recaptured. Of the 21 females transferred (excluding small juveniles) 13 (62%) homed, 1 (5%) possibly homed, 1 (5%) failed to home, and 6 (28%) were not recaptured.

Mice not transferred.—On August 29, when the mice collected in the outer square were transported before release, those collected in the 76 traps of the inner squares were released at the place of capture. This group comprised 42 mice, 22 males and 20 females. Thirty-nine (20♂♂, 19♀♀) were adult and subadult animals. Three (2♂♂, 1♀♀) were very small juveniles. In the second period 18 of the 20 adult and subadult males and all of the 19 females were retaken. None of the juveniles was retaken.

Of the 20 males released at the site of capture (excluding small juveniles), 15 (75%) were taken in the same or adjacent traps each period, 3 (15%)

were taken in traps 110-173 feet apart in the two periods, and 2 (10%) were not retaken. Of the 19 females, 18 (95%) were taken in the same or adjacent traps and 1 (5%) was taken in traps 110 feet apart. None failed to be retaken.

DISCUSSION

In the present study the males homed more successfully than the females: 89% of the transferred males returned home or to a closely adjacent area while only 67% of the females did so. One male and one female definitely failed to home and were recaptured far from their original homesites.

The contrasting behavior of males and females is also shown by comparing the records of the mice transported before release with the records of the mice released at the site of capture. There were similar percentage recaptures of the males of both groups; 93% of the transferred males and 90% of the non-transferred males were recaptured in the second period. The records for females were not so nearly alike, for only 72% of the transferred females were retaken while 100% of the non-transferred females were retaken.

A large percentage of the transported mice of both sexes returned home. The homing of a greater number of males than females is probably related to the fact that the normal range of males exceeds that of females.

Under normal conditions individual mice occasionally travel some distance from their homes and then return to them (Blair 1943; Storer, Evans, and Palmer 1944). This might be considered evidence that mice are familiar with an area somewhat greater than their normal ranges, and so provide an explanation of the homing ability. However, there is no data to show that exploratory trips are sufficiently numerous and varied in direction to make the majority of mice familiar with large surrounding areas. Homing over even relatively short distances would require familiarity with rather large areas: homing from a distance three times the normal home range diameter would mean familiarity with an area roughly nine times the size of the home range. Familiarity with an area this size is of course not impossible. In the experiments of the Muries the majority of mice, including young adults still in gray pelage, returned home from distances ten or more times their normal range diameters. It is difficult to believe mice could have been familiar with areas 100 or more times the size of the normal ranges.

Whatever the explanation of the ability, the *Peromyscus* observed in the present study showed a distinct homing tendency. A high proportion of both sexes returned home from distances several times their normal cruising ranges. The return trips were made through a broad zone of occupied ranges. Neither the presence of recently vacated ranges in all directions nor the existence of similar habitat in all directions caused failure of the homing ability. In the present study at least, these factors appear to be ruled out as important aids to the homing.

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Studies on the Parasitic Helminths of the North Central States. II. Helminths of Voles (Microtus spp.) Preliminary Report

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The helminths of North American mouse-like rodents have received little study. Previous work has been based on low numbers of animals examined, and there has been little reference to the ecology involved. The purpose of this paper is to present data resulting from the examination of over 600 voles, with special reference to host-parasite relationships.

Hall (1916) reviewed the nematodes parasitic in rodents, and previous records of helminths from voles are contained in the papers of Harkema (1936) and Erickson (1938). In addition to these, a number of new species has been described. No effort has been made here to list all helminths previously recorded from voles, and only those of interest in connection with the present work are mentioned.

Rodents of the genus *Microtus* are of much economic importance in connection with agriculture, and for this reason have been given considerable attention. The fluctuations of vole populations have long been observed, and a considerable amount of effort has been spent in attempts to explain their population behavior. The bionomics of voles has been investigated both in North America and in Eurasia. The work of Hamilton (1937, 1941) in the eastern United States has been especially complete, as has that of Elton and his co-workers in Europe. Much work on the ecology of rodents has been done in Russia, some of which has been reviewed by Kalabukhov (1935), and by Elton (1942). Unfortunately, the Russian work has not been generally available.

Voles lend themselves especially well to studies concerned with population fluctuations, since the rise and fall of their numbers seems to occur within a span of three or four years, in contrast to that of certain other species (snowshoe hare, ruffed grouse, and others), which have a cycle of about 10 years.

In spite of their availability in considerable numbers, wide geographical distribution, and interesting population behavior, very little has been done in the way of host-parasite studies with voles. The work of Kirschenblatt (1938), concerning *Microtus socialis satunini* Ogn., *M. socialis schidlovskyi* Arg., and *M. arvalis transcaucasicus* St., as well as other rodents in the

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Transcaucasus region, is of especial interest. We were able to obtain this paper only in late 1947, through the kindness of Dr. Charles Elton, as it does not appear to be available in North America. An effort has been made to include the points in Kirschenblatt's work which are of interest in connection with the present paper. According to Dr. H. A. Baylis (personal communication), voles in the British Isles have not been found parasitized by helminths to a degree adequate to allow a profitable study of this type. Elton and his associates (1931) carried out such a study with the woodmouse, *Apodemus sylvaticus* L., a form in some ways comparable to the North American *Peromyscus*.

METHODS AND SOURCES OF MATERIAL

The procedure for collecting helminths was the same as that used in a previous study (Rausch and Tiner, 1948). After the voles were weighed, the viscera were removed, and each organ was opened separately in a clean dish of water. The contents of each viscus were examined under the low power of the dissecting microscope, after any macroscopic forms present had been removed. It should be noted here that all the animals examined were in a fresh condition; in the opinion of the writers, carcasses preserved in formalin do not give satisfactory results, although the use of preservatives may be necessary under some circumstances. After their isolation, the helminths were fixed in formalin-acetic acid-alcohol solution, and handled in the usual manner.

Voles were ordinarily captured by means of snap mouse traps, set directly in the runways. Baited traps were rarely used.

The collecting was done entirely by the senior author from 1942 to 1945. From 1945 to 1948, assistance was given by the junior author, and by other persons as noted in the acknowledgment. Some of the latter, particularly Messrs. L. H. and C. F. Troesch, have lent their assistance on occasion since the inception of this study. The Wisconsin collecting, in connection with this study, was done by the senior author.

The present study is concerned mainly with a general survey of the helminths parasitic in voles, and with more intensive work carried out locally in two areas.

For the survey work, voles were obtained from wherever possible, and specimens were secured from the states of Ohio, Indiana, Illinois, Michigan, and Wisconsin. The number of animals from Indiana and Illinois, however, was relatively small. A few voles were examined from Manitoba, in addition to those from the North Central States region. While the Manitoba specimens do not come under the scope of this study, helminth records from them are included in order to give all possible information on distribution.

A total of 648 voles has been examined. Of these, 570 were *Microtus p. pennsylvanicus* Ord; 46 were *M. ochrogaster* Wagner; and 32 were *M. pennsylvanicus drummondii* (Audubon and Bachman).

The localities in the North Central States region from which voles have

been obtained are shown in Figure 1, according to county in which they were found. These counties, as numbered on the map, are as follows:

WISCONSIN
1. Vilas
2. Fond du Lac
3. Sheboygan
4. Dodge
5. Dane
6. Waukesha
7. Milwaukee

ILLINOIS
8. Cook
9. Hancock
10. Mason
11. Piatt
12. Champaign
13. Vermilion
14. Saline

INDIANA
15. Tippecanoe

MICHIGAN
16. Cheboygan
17. Ingham
18. Washtenaw

OHIO
19. Preble
20. Franklin
21. Union
22. Marion
23. Morrow
24. Lorain
25. Geauga

Of the two local intensive studies, one was carried out in Ingham County, in southern Michigan (Figure 1, county 17). A fairly uniform field of about 23 acres, adjoining, on the west side, an extensive woodlot, was used.

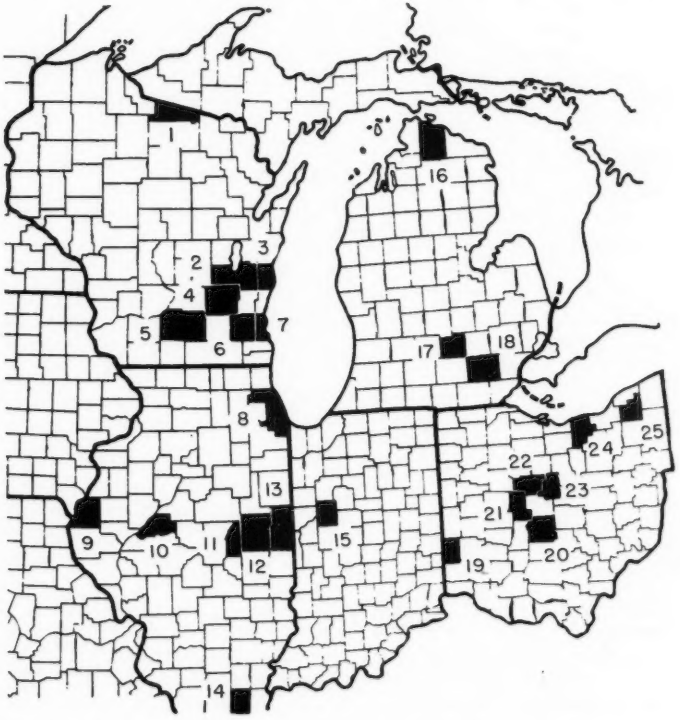

Fig. 1.—Map of the North Central States region, showing counties from which voles were collected.

An open woodlot about 50 yards wide ran across the south side of the field, while the other two sides bordered cultivated fields. The vegetation of the area consisted of blue grass, *Poa* sp., with several species of annuals interspersed. Hawthorne bushes, *Crataegus* sp., were distributed throughout, as were small areas of prickly ash, *Zanthoxylum americanus* L., and *Vibernum* sp. Certain moist areas supported heavy growths of *Carex* sp., which also appeared to be good vole habitat, especially during the winter. As far as could be determined, the vole population was uniform over the area when the study was begun. The field was grazed by cattle during the late spring and summer.

The larger woodlot, adjoining the west side of the field, contained about 69 acres, and was of beech-hard maple type. Several areas within it were quite low, and supported heavy growths of *Cephalanthus occidentalis* L. and *Typha latifolia* L., among a variety of plants. Since this woodlot had been ungrazed for a number of years, and since conditions in general were favorable, several species of mammals were abundant. No mammals had been removed by hunting or trapping for a period of years preceding this study. As will be explained further below, the helminths of the mammals resident in this woodlot were rather intensively studied, along with those of the voles from the nearby field.

The voles were trapped from different parts of the area in an effort to distribute the population losses due to trapping evenly over the whole area, thereby minimizing the effort upon vole densities, and, in turn, upon the results obtained. It was the plan to trap 30 voles each month, as well distributed over this period as possible. A total of 345 voles was obtained from the field, over a period of 13 months. Figure 2 shows the age composition of these animals, according to percentage of the total in each weight group.

Observations on the helminths of this area were begun in July, 1945, and were carried on through July, 1946. The voles approached and passed a peak in population density during the time of the study, with the decline occurring

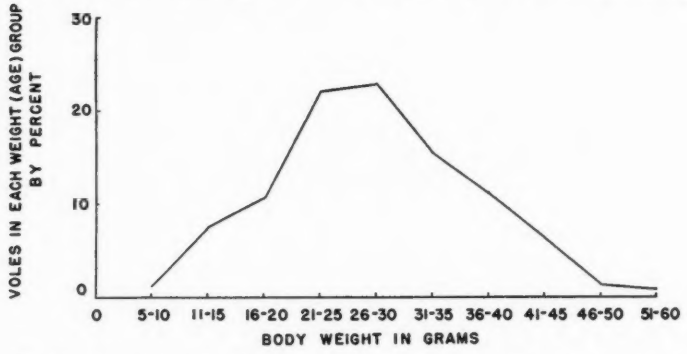

Fig. 2.—Age composition of the 345 voles collected on the southern Michigan study area.

about May, 1946. Observations of others sustained this conclusion. According to Dr. D. W. Hayne (personal communication), this population peak was unusually high — the highest since the year 1937. While no absolute census figure for the area was obtained, it was obvious that the voles were at first very numerous, as attested by well-worn runways, abundant, fresh cuttings, and fecal deposits. Also, the voles could often be seen in places where the vegetation was not too abundant. The high population level persisted through the winter of 1946, but a precipitous decline was noted in the spring, as mentioned above. From the time of the decline on, specimens were obtained only with much difficulty.

The contrast during the late spring of 1946 to conditions of the previous year was indeed great. Runways had become poorly defined from disuse, and cuttings and feces were not to be seen. This population decline took place early, before prolonged dry weather could have reduced breeding activity. No evidence as to the cause of the decline was obtained. In May, 1947, we again trapped in this study area, and it was evident that the vole population was still low. Since no trapping had been done there during the previous year, the population was undisturbed during this period.

The ecology of the helminths of voles, or of any other given host, will never be adequately understood if the particular host in question is the only one examined from areas under investigation. It is probably safe to assume that a mammal resident in a given area must suffer a degree of exposure to helminth species which infect it rarely or not at all. Much can be learned of the interrelationships involved when it is known just which host species and which parasites are present in a given area. We have, therefore, attempted to sample the *total* parasitic helminth fauna of areas studied, whenever it was possible to do so. To date this holds true for areas in Ohio, Michigan, and Wisconsin; there was little opportunity to study other than voles from the areas in Illinois and Indiana. Of the many birds and mammals examined during the course of these studies, most will be considered in future reports. However, additional information is given here for two areas where intensive studies were carried out.

From the Michigan study area (Figure 1, county No. 17), the following resident mammals were examined: opossum, *Didelphis v. virginianus* Kerr; short-tailed shrew, *Blarina brevicauda kirtlandi* Bole and Moulthrop; raccoon, *Procyon l. lotor* Linnaeus; long-tailed weasel, *Mustela frenata noveboracensis* Emmons; skunk, *Mephitis mephitis nigra* Peale and Beauvois; house cat, *Felis domesticus* Linnaeus; woodchuck, *Marmota m. monax* Linnaeus; chipmunk, *Tamias striatus rufescens* Bole and Moulthrop; red squirrel, *Tamiasciurus hudsonicus loquax* Bangs; fox squirrel, *Sciurus niger rufiventer* Geoffroy; eastern flying squirrel, *Glaucomys v. volans* Linnaeus; prairie white-footed mouse, *Peromyscus maniculatus bairdii* Hoy and Kennicott; northern white-footed mouse, *P. leucopus noveboracensis* Fischer; meadow vole, *Microtus p. pennsylvanicus* Ord; pine vole, *Pitymys pinetorum scalopsoides* Audubon and Bachman; house rat, *Rattus norvegicus* Berkenhout; house mouse, *Mus musculus* Linnaeus; jumping mouse, *Zapus hudsonius breviceps* Bole and Moul-

throp; cottontail, *Sylvilagus floridanus mearnsii* Allen. The host names for the Michigan mammals are according to Burt (1946).

Host-parasite relationships as observed on the Michigan study area are shown in Figure 3 (parts A, B, and C). Cestodes, trematodes, and nematodes respectively are tabulated so as to show the host species infected by each parasite, and their relative abundance in these hosts. Only resident mammals trapped in the field or woodlot are considered. It can be expected, in the case of this study area, that the voles were only rarely exposed to helminths infecting some of the mammals living in the woodlot. However, some of the woodlot inhabitants tended to range outward into the surrounding fields. Only two meadow voles were collected well inside the woodlot, and neither was infected with helminths. Only a few mammals were regularly taken in the field, along with the voles; they were jumping mouse, short-tailed shrew, prairie white-footed mouse, and house mouse.

For the intensive study area in Wisconsin, a large marsh of about 350 acres was chosen (Figure 1, county No. 5). This marsh was a rather uniform biotic community, isolated to a considerable degree by the surrounding higher, heavily cultivated agricultural land. A spring-fed creek flowed through the area, and this was further fed by springs arising within the marsh itself. The surface of the smaller creeks bore dense growths of water cress, *Radicula* sp. The marsh vegetation consisted to a large extent of *Phragmites communis* (Reed), *Typha latifolia* L., and *Carex* spp., interspersed with some *Aster* spp., *Solidago* spp., and other plants. The creek banks were grown to willow, *Salix* sp., while other higher areas supported elderberry, *Sambucus canadensis* L., giant ragweed, *Ambrosia trifida* L., and nettle, *Urtica gracilis* Ait.

This area was relatively undisturbed by man, since no hunting or trapping had been done for some years, and it was not used for any agricultural purpose; consequently, mammals were abundant here. This area in some ways was more interesting than the Michigan area, since the voles occurred within the marsh itself, and their contact with the other mammals must have been more immediate.

Although mammals were numerous in the marsh, the number of species here was smaller, limited in this respect by the much more uniform habitat. The following mammals, resident within the marsh, were examined: opossum, *Didelphis v. virginianus* Kerr; short-tailed shrew, *Blarina b. brevicauda* (Say); common shrew, *Sorex c. cinereus* Kerr; raccoon, *Procyon l. lotor* Linnaeus; least weasel, *Mustela rixosa allegheniensis* (Rhoads); mink, *mustela vison letifera* Hollister; skunk, *Mephitis mephitis avia* Bangs; house cat, *Felis domesticus* Linnaeus; woodchuck, *Marmota monax* Linnaeus ssp.; prairie white-footed mouse, *Peromyscus maniculatus bairdii* Hoy and Kennicott; meadow vole, *Microtus p. pennsylvanicus* Ord; muskrat, *Ondatra z. zibethica* Linnaeus; house mouse, *Mus musculus* Linnaeus; cottontail, *Sylvilagus floridanus mearnsii* Allen. In addition to the above, the short-tailed weasel, *Mustela c. cicognanii* Bonaparte, was also resident here, but none of these was collected. The sub-specific status of some of the Wisconsin mammals is not entirely clear at present.

The host-parasite relationships of this marsh were particularly interesting, to a large degree because of the closer contacts of the mammals with one another, as mentioned above. Figure 4 (parts A, B, and C) presents a general picture of these interrelationships. A single house mouse, infected with *Aspiculuris* sp., was collected after Figure 4 was prepared.

Of the mammals present in this area, only the muskrat was rather closely related to the vole (i.e. both of the subfamily Microtinae). If there were any sharing of the helminth parasites by the different host species, one might expect this to occur between the two microtine rodents, while parasite faunas would be shared to a much lesser degree by more distantly related hosts. The results of our examinations indicated that weaknesses in host specificity barriers were not necessarily related to the amount of phylogenetic separation of the hosts.

Thus, we found *Trichuris opaca* Barker and Noyes, 1915, and *Hymenolepis evaginata* Barker and Andrews, 1915, infecting both the muskrat and the vole. The four specimens of the latter cestode taken from voles appeared to be abnormal in development, however, as will be discussed further below. *Entosiphonus thompsoni* Sinitsin, 1931, an abundant parasite of the short-tailed shrew, an insectivore, was encountered in three voles. *Quinqueserialis quinqueserialis* (Barker and Laughlin, 1911) was a common parasite of the muskrat, but did not occur in voles; the latter were commonly infected with a related species, *Q. hassalli* (McIntosh and McIntosh, 1934). *Quinqueserialis hassalli* has been recorded from the woodchuck from the same marsh area (Rausch and Tiner, 1948); however, comparison with specimens collected here from voles indicates that the worms from woodchucks should be considered only as *Quinqueserialis* sp. until additional material is available for study. In general, the findings relative to host specificity appear to parallel those recorded in a previous paper (Rausch and Tiner, 1948). Further data on this are given below, in the discussions of the separate helminth species.

REMARKS ON THE BIOLOGY OF THE HOST

It seems expedient at this point to include some information on the bionomics of voles. This has been obtained mainly from an examination of the literature, although some of our own observations have been included. Most of the observations made by various workers in the United States have been based on the common meadow vole, *Microtus p. pennsylvanicus*. Such information may be of use in better evaluating the results of our investigations.

Voles of the genus *Microtus* are herbivorous mammals, common in both North America and Eurasia. They feed essentially on grasses, and to a lesser degree upon grain, tree bark, tubers, and other vegetable matter. In the North Central States, during the winter months, they are often found in corn shocks. As far as we have been able to learn, voles ingest very little animal matter.

Voles have a characteristic rapid rate of reproduction, and a short life span. According to Hamilton (1937), who studied the common meadow vole, growth is very rapid until about the 12th week, when it is retarded and

the animals are considered mature. Bailey (1924) found that female voles may be sexually mature at 25 days of age, while the males may be fertile at 45 days of age. According to the data presented by Hamilton (1937), age and weight of voles are closely correlated, allowing one to determine rather closely the ages of animals examined. This would be of value if an attempt were made to learn something of the effects of host age on helminth infections in these animals.

The older animals apparently die each year during the late summer or fall, and only the animals born late in the season are able to survive the winter. Baker and Ransom (1938) found, with *Microtus agrestis* L. in Europe, that the older animals die in about October. We have found very few large adults during the winter months over the region where this study was made; the great majority of animals consisted of subadults. We found this to be true even during the times of high population density. We did observe, however, in *Microtus pennsylvanicus drummondii* and *M. ochrogaster*, that large adult animals were present during the winter months of 1947-48, even though the populations were known to be quite low.

Hamilton (1937) listed three factors as contributing to the short life span of the vole: 1) the attainment of sexual maturity at a very early age; 2) extreme prolificacy; 3) little cessation of activity in the search for food. According to the same author (1941), the length of the breeding period of voles in the eastern United States is correlated with population density; breeding may continue on through the winter when the population density is nearing the peak. Hamilton also stated "the number of young in a litter varies with the population level of the mice, large litters predominating when mice are abundant."

Population densities and reproductive activity in voles differ greatly from one area to another at the same time. For example, it was seen, during the winter of 1947-48, that *Microtus p. drummondii*, in Manitoba, and *M. ochrogaster*, in Indiana and Illinois, were breeding at a high rate. This occurred, even though the voles were at a low point in population density. In Wisconsin, on the other hand, where a large number of voles was examined during the same period, not a single large adult was observed. Furthermore, examination of the trapped animals failed to disclose perforate vaginae, placental scars, pregnancy, or evidence of any breeding activity in the males. We are of the opinion, therefore, that nearly all the animals present at this time were nonbreeding adults.

It should not be assumed, however, that these observations on *Microtus p. drummondii* and *M. ochrogaster* are necessarily comparable to those made previously on *M. p. pennsylvanicus*.

RESULTS

The various helminth species obtained are discussed separately below. The numbers in parentheses following the parasite name refer to Figure 1, in which the distribution of the helminths is shown. In showing this distribution, the species of *Microtus* is not considered; however, Table I lists the parasites according to host species in which they occurred, along with certain other data.

CESTODA

In general, cestodes of the family Anoplocephalidae Fuhrmann, 1907, are common parasites of voles, while cestodes belonging to other groups are rare. This appears to be true of the cestodes of Eurasian voles, as well.

ANOPLOCEPHALIDAE

1. *Andrya macrocephala* Douthitt, 1915. (Fig. 1, counties 12, 17, 20, 21).—First described from *Geomys bursarius* (Shaw), this cestode is a common parasite of voles, from which it has been recorded by Rausch (1947). Although *Andrya* spp. have previously been recorded from *Microtus,* specific determinations were not made. Erickson (1938) recorded *Andrya* sp. from *Microtus p. pennsylvanicus* and from *Clethrionomys g. gapperi* Vigors; however, according to his description ("a short broad cestode was removed from the cecum . . ."), he apparently was dealing with a species of *Paranoplocephala* Luehe, 1910.

Another species, *Andrya primordialis* Douthitt, 1915, has also been recorded from voles. Rankin (1945) recorded this cestode from *Microtus longicaudus* (Merriam) and from *M. montanus* (Peale), from the state of Washington. Douthitt (1915) recorded it from *M. p. modestus* (Baird), from Colorado. It seems evident that *A. primordialis* is rare or does not occur in the region where the present study was made.

Although we have not recorded *Andrya macrocephala* from a number of localities from which voles were examined, it is, nevertheless, very common in some areas. Since some of our collections from certain areas were made during the winter months only, when this cestode is rarely found, it is probable that the examination of voles collected during the summer months would show it to be common in other areas also. It might be mentioned here that *Geomys bursarius,* from which it was described, and of which it seems to be a common parasite (Douthitt, 1915) is found only over the western edge of the region considered in this study. Except for a specimen of *Microtus p. drummondii,* which contained 6 worms (5 of which were immature), no more than 4 worms were removed from a single host. The average number per infected animal, based on 345 voles from southern Michigan, was 1.6 worms.

Data obtained from the Michigan study area make apparent certain characteristics of *Andrya macrocephala* infections in the common vole. The peak of infection was observed to occur during the month of August, with very little parasitism by this cestode during the winter months. Figure 5 shows the course of such infections. Immature worms were again found in the spring, suggesting that the infected intermediate hosts are rarely available to the voles during the winter. No differences in age susceptibility were observed.

The life cycle of cestodes of the genus *Andrya* remains unknown, but it would seem likely that mites serve as the intermediate host, in view of our knowledge of the life cycles of other members of the sub-family. The ecology of such mites would be of much importance in the epizootology of the cestodes for which they serve as intermediate hosts. Krull (1939) found that oribatid mites, which serve as the intermediate hosts of *Moniezia, Cittotaenia,* and

others, were most abundant on grass after a heavy rain, and that they retained their greatest constancy where moisture was abundant enough to encourage grass growth. According to the same author, the mites are not reduced greatly by cold, wet weather of a week's duration, or by a dry period of a month's duration, provided these changes occur during the spring or early summer. Krull also found that the mites were more abundant in the spring than in winter, and that they were more abundant on the grass early in the morning than they were during the day. The peak abundance of such mites on grass probably corresponds closely to the period of greatest activity of the voles. It seems probable that mites would often be ingested with the grass upon which voles feed.

It is of interest to note the resemblance of the course of infection of *Andrya caucasica* Kirschenblatt, 1938, in *Microtus socialis,* to that of the present species in *M. p. pennsylvanicus* (Kirschenblatt, 1938; graph 6, page 22). In both cases, infections were low during the winter months. Kirschenblatt also reported a low average number of worms (less than 2) per infected host. One might say that *A. caucasica* in the Transcaucasus region fills an ecological niche very similar to that occupied by *A. macrocephala* in north-central North America.

2. *Andrya microti* Hansen, 1947. (5).—A single cestode referable to this species was collected during February, 1948, at Madison, Wisconsin. Hansen (1947) described *A. microti* from *Microtus ochrogaster* in Nebraska. Recently, through the kindness of Dr. Reinard Harkema, we had the opportunity of examining what appears to be this species from the cotton rat, *Sigmodon h. hispidus* Say and Ord. The infected animals had been collected in Wake County, North Carolina. This species is uncommon in the North Central States region, according to the results of the present study.

There is a striking morphological similarity between *Andrya caucasica* Kirschenblatt and *A. microti;* however, evidence is hardly adequate at present to consider them identical. As far as we have been able to observe so far, cestodes of the genus *Andrya* are not affected morphologically by the host species in which they occur. It seems, however, that the rather closely related species found in North American rodents (*A. macrocephala* Douthitt, 1915); *A. microti* Hansen, 1947; *A. ondatrae* Rausch, 1948) should be carefully studied when a large volume of material becomes available for comparison.

3. *Andrya* sp. (17, 20).—Five specimens of cestodes of the genus *Andrya* were obtained from voles collected in central Ohio and southern Michigan. None of these contained gravid segments, although mature segments were present. The material was not adequate to allow for specific identification, although it is possible that these represented atypical specimens of *A. macrocephala.* Morphologically they did not agree closely with this species, however.

4. *Paranoplocephala troeschi* Rausch, 1946. (1, 4, 5, 6, 8, 16, 17, 18, 21, 22).—Found in or near the cecum of the host, this cestode was the most common found parasitic in voles. Hansen (1947) reported *P. troeschi* from *Microtus ochrogaster* from Nebraska, and it is possible that the previously

mentioned "*Andrya* sp.," recorded by Erickson (1938), was identical with this species.

The maximum number of this species of cestode obtained from a single host was 8, with an average (based on 345 animals from the Michigan study area) of 2.2 per infected animal. As far as could be determined, host age has little or no effect on infections with this cestode. These cestodes appear to be eliminated from the host during the months of early spring (i.e. previous to the first of June).

It was of interest to note that the heaviest infections with this parasite were observed during the winter months, with the highest percentage of animals infected during the months of December and January (see Figure 5).

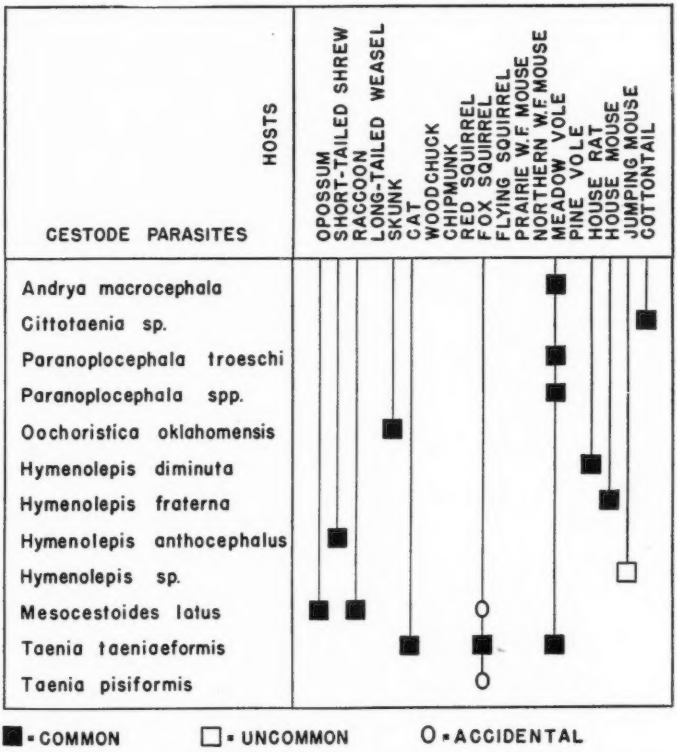

Fig. 3.—Host-parasite relationships on the Michigan study area. Part A. CESTODA.*

* The helminth names used in these charts have been checked, and, as far as could be determined, are valid.

During the course of this study, this cestode was not collected from voles before the month of October, or after the month of May. While occasional infections may occur during the warmer months of the year, they must indeed be rare.

Very small specimens of *Paranoplocephala troeschi*, with only the beginning of strobilae, were found during the earlier part of the winter. It was also noted that immature worms were found in larger numbers in a single host animal than were those with gravid segments. This suggests that only a few worms may be able to survive, even though the initial infection be much heavier. We did not find any immature worms after the month of February. This cestode must mature very rapidly, and must have a very short life span.

It would also seem that mites function as the intermediate host of *Paranoplocephala troeschi*, although there is no definite evidence for such an assumption. It appears that the intermediate host of this cestode is not available to

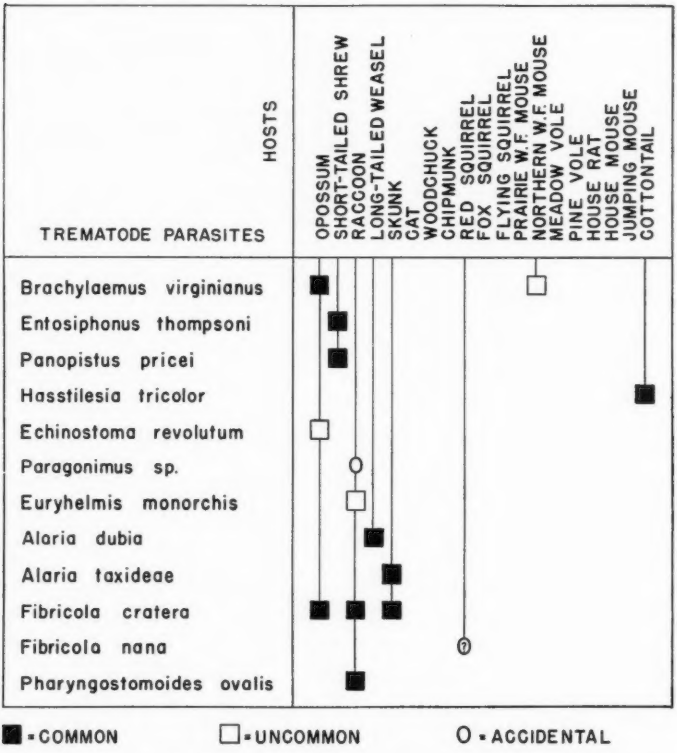

Fig. 3.—Host-parasite relationships on the Michigan study area. Part B. TREMATODA.

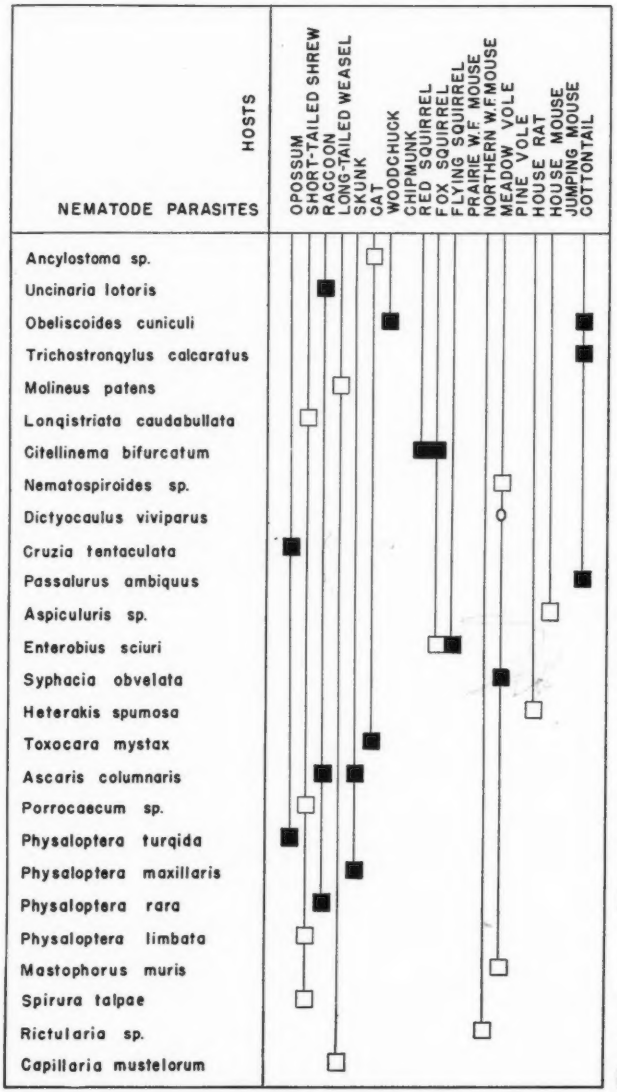

Fig. 3.—Host-parasite relationships on the Michigan study area. Part C. NEMATODA.

the voles during the warmer months of the year, and this is suggestive of some very interesting ecological factors upon which this must be dependent. Whether these factors are connected with seasonal variation in host behavior, or with physiological or immunological peculiarities of the definitive host, is unknown.

Paranoplocephala troeschi is morphologically very close to *P. brevis* Kirschenblatt, 1938. Although Kirschenblatt's paper was cited at the time *P. troeschi* was described (Rausch, 1946), it was not yet avalaible. It can be seen that these worms appear to fill similar ecological niches in their respective regions of distribution, and this may be very important in establishing relationships. Kirschenblatt's graph 3 (page 18) gives some information on the behavior of *P. brevis* in the host (*Microtus*). It is probable that further study will show that *P. troeschi* should be considered a synonym of *P. brevis*; however, additional material for comparison is needed to establish this.

5. *Paranoplocephala* spp. (1, 2, 3, 4, 5, 10, 12, 14, 16, 17, 18, 21, 22).—When *P. troeschi* was described the attendant examination of a fairly large series of cestodes from voles revealed that specific differences often were most difficult to delineate in the genus *Paranoplocephala*. This, with the present confusion of names, would indicate that further work on this group is badly needed. We expect to present further data on this problem in the future. Because of the present status of these cestodes, specific determinations are not indicated here.

A large species of *Paranoplocephala* was occasionally found in the duodenum of the host, just below the stomach. In no case was more than a single worm found per host animal. What appears to be another species was found lower in the small intestine. In general, these cestodes were uncommon in voles, and nothing was observed concerning their epizootology.

DILEPIDIDAE

6. *Choanotaenia* sp. (12).—A single worm belonging to the genus *Choanotaenia* Railliet, 1896, was removed from the intestine of a specimen of *Microtus ochrogaster*, collected at Champaign, Illinois. The hooks appeared to be 26 in number, and were arranged in a double row; they averaged 30 μ in length. The testes averaged 31 in number, and the cirrus sac measured from 80 to 115 μ in length. No gravid segments were present. This may represent an accidental infection.

HYMENOLEPIDIDAE

7. *Hymenolepis fraterna* Stiles, 1906. (21).—A single cestode, without a scolex, was obtained from a vole collected near Marysville, Ohio. It seemed to agree in all respects to *H. fraterna*. *Hymenolepis fraterna* was commonly seen as a parasite of the house mouse, but it cannot be considered a common parasite of the voles of this region. Hughes (1940) recorded this cestode as occurring in a European vole, *Microtus agrestis* L., however.

8. *Hymenolepis evaginata* Barker and Andrews, 1915. (5).—Two voles,

each containing two cestodes of this species, were collected on the southern Wisconsin study area. Although a common parasite of muskrats over the North Central States region, it must be considered accidental in voles.

The cestodes from the voles were rather small for this species (80 to 130 mm), but in general were typical in their morphology. However, it was noted that in no case had any eggs developed, although proglottids had been shed from all four strobilae. This is perhaps further evidence that the vole is an abnormal host for this parasite.

9. *Hymenolepis* sp. (13).—Five specimens of a cestode belonging to this genus were obtained from a vole collected in eastern Illinois. Unfortunately, the hooks had been lost from the scolices, and the material is not considered adequate for specific identification.

TAENIIDAE

10. *Taenia taeniaeformis* (Batsch, 1786). (1, 8, 12, 17, 22).—Strobilocerci of this cestode were rather common in the liver of voles from some areas. The distribution was, however, quite local. This is not readily understood, since there must be little difference in the house cat population over the region under consideration. Feral cats were present over most of the areas considered, and, in most cases, vole habitat areas were readily accessible to cats from nearby farms. In northern Wisconsin (Figure 1, number 1) where rather a high incidence of infection was observed, it is possible that the bobcat, *Lynx rufus* Schreber, might also have acted as the definitive host for this cestode. Rollings (1945) reported *Taenia taeniaeformis* to be a fairly common parasite of the bobcat in Minnesota. No information is yet available on Wisconsin bobcats.

On the Michigan study area these larval cestodes were first seen in voles in November, and during each month thereafter until the last of May. The largest percentage of infected animals was seen during the month of January. A somewhat parallel situation was observed in the fox squirrel, concurrently trapped in the adjacent woodlot, although a smaller number of animals was infected (Rausch and Tiner, 1948). In the voles from this area the maximum average number of cysts per animal per month coincided with the peak in incidence of infection. Although this parasite was found in the liver of a muskrat from the southern Wisconsin study area, it was not observed there in voles. Feral house cats, collected on the immediate study area, were found to be infected with cestodes of this species, and other cats, not captured, were from time to time seen on the area.

A total of 26 house rats was examined from a farm in central Ohio, and it was found that 21 of these were infected with larval cestodes of the present species. A total of 35 voles examined from the same farm area failed to disclose any infections by this parasite. Egg density per given unit area probably decreased very rapidly as distance from the farm buildings increased. Unfortunately, enough rats living in the fields away from the buildings could not be obtained to allow for a comparison under these conditions.

A cysticercus belonging to the genus *Taenia* was taken from the liver of a specimen of *Microtus p. drummondii*, collected near Winnipeg, Manitoba.

This cysticercus was not identified to species. Two rows of hooks were present, with 12 in each row. The larger hooks averaged 72 μ in length, while the smaller ones averaged 49 μ.

11. *?Cladotaenia* sp. (5, 13, 17, 21).—A few voles were found to be infected with very small cysticerci, which occurred in the liver. Two specimens from voles collected in southern Michigan had hooks about 16 μ in length, arranged in a double row.

On the southern Wisconsin area, a relatively heavy infection was noted. Of the 43 voles taken on the marsh, 12 were infected, with an average of 3 cysts per infected animal. The hooks of these, also arranged in a double row, measured about 23 μ in length. The liver cysts were quite small, and commonly measured about 2 mm. in diameter. With the possible exception of one muskrat, no other host animal from this area was found infected by these cysticerci.

It is possible that these cysticerci were larval cestodes of the genus *Cladotaenia*; it is hoped that this can be determined by feeding experiments with hawks. In the Wisconsin marsh, hawks (*Circus, Buteo, Accipiter*) were usually abundant, and perhaps conditions in this area allowed a better opportunity for vole infections with this parasite. Experimental work by one of us (R. R.) has shown that these cysts are not larvae of owl cestodes (*Paruterina*); this work will be reported separately.

TREMATODA

During the course of the present study, only two species of trematodes were found which could be considered natural parasites of voles. One of these, *Quinqueserialis hassalli* (McIntosh and McIntosh, 1934), was widely distributed, and occurred in a number of localities where habitat seemingly was favorable to the intermediate host. A second, *Mediogonimus ovilacus* Woodhead and Malewitz, 1936, was recorded only from Washtenaw County, Michigan, from which locality it was first described. Three infections by a third species, *Entosiphonus thompsoni* Sinitsin, 1931, could only be regarded as accidental. Price (1931) reported *Microtus pennsylvanicus* to be the natural host for *Schistosomatium douthitti* (Cort, 1915); it is possible that we have overlooked infections of this parasite.

That voles have few trematode parasites is not surprisinig, considering their diet, and the fact that in general they inhabit areas which are not favorable habits for snails.

NOTOCOTYLIDAE

12. *Quinqueserialis hassalli* (McIntosh and McIntosh, 1934) (4, 5, 15, 18, 21).—The only common trematode found in voles, this species appeared to be abundant only locally, although it has been recorded from voles over a wide geographical area (Harwood, 1939). The distribution of this parasite seems to be limited to areas with aquatic habitat suitable for a snail intermediate host.

On the southern Wisconsin marsh, a high percentage of voles (46 per cent) was infected. The trematodes averaged 8 per infected host, with a maximum number of 37 in a single host. Muskrats were not found to be infected with

this parasite; they were, however, heavily infected with a member of the same genus, *Quinqueserialis quinqueserialis* (Barker and Laughlin, 1911). The latter occurred in very large numbers (average for 6 infected muskrats: 406 worms). More than a thousand of these trematodes were removed from the cecum of a single muskrat.

Voles trapped on the Wisconsin marsh during the winter months were found to be heavily infected by *Quinqueserialis hassalli*. Whether these infections had carried over from the previous fall, or whether they obtained during the winter months, is not known. A few immature trematodes found during January and February indicated that infective stages were available to the voles to at least some degree during the winter. It might be mentioned here that open water was always present in this marsh, because of the continual flow from the springs. Although the investigation here has so far been carried through only one spring season, evidence so far would indicate that there is a decrease in infection by this parasite during this time.

PLAGIORCHIIDAE

13. *Mediogonimus ovilacus* Woodhead and Malewitz, 1936. (18).—Two of four voles secured from Washtenaw County, Michigan, were infected by this helminth. This species appears to be very restricted in its distribution, since we did not encounter it elsewhere in the region considered. In one case, more than 50 worms were taken from cysts in the liver of a young vole (28 grams), while 3 specimens were taken from the bile duct of a second animal. In the first case, a few of the trematodes had migrated through the bile duct into the small intestine, probably after the death of the host. Our observations on this species agree with those made by Woodhead and Malewitz (1936). We observed also that the mature worms in the case of the heavier infection were much smaller than were those from the bile duct of the second animal. The infected animals were captured along a river.

Part of the liver of the animal showing the heavier infection was sectioned, and a few observations were made on the reaction of the host tissue to this parasite. The worms had been well walled off, and were surrounded by a capsule of connective tissue. Many eggs, found outside the capsule, were also being walled off, and a heavy deposition of a black pigment was seen in the area with the eggs. There was a metaplasia of the biliary epithelium, and some pressure necrosis of the liver cells. The cellular reaction was moderate, consisting mainly of macrophages. Eosinophiles were not observed. This appeared to be the most pathogenic parasite encountered by us during the course of the present study, although it does not seem probable that there would be any serious result to the host, unless infections were extremely heavy. A photomicrograph of a typical liver section is given in Figure 6.

BRACHYLAEMIDAE

14. *Entosiphonus thompsoni* Sinitsin, 1931. (5).—This trematode was taken only from the voles of a single locality, and must be considered purely accidental in the vole. Two of the infected voles contained a single worm each,

while a third harbored two worms. The worms appeared to be normal in development; all were mature, with numerous eggs in the uteri.

Entosiphonus thompsoni was a very common parasite of the short-tailed shrew over the entire region considered in this study. However, the short-tailed shrew was not abundant in the marsh from which the infected voles were taken. Another shrew, *Sorex c. cinereus*, was quite abundant in the area, but only on one occasion was this species found to be infected with *E. thompsoni*; in this case, a few small, immature worms were collected. Krull (1933) has recorded this trematode from the white-footed mouse, *Peromyscus leucopus noveboracensis*.

NEMATODA

Nematodes were found to be very common parasites of voles, although they differed considerably in variety and number from one area to another.

TRICHOSTRONGYLIDAE

15. *Nematospiroides* sp. (5, 17, 18).—This nematode was taken from 9 animals of the 345 examined from the southern Michigan study area, and from 27 of the 43 voles from the Wisconsin study area. In general, it was an uncommon parasite. The number of worms per infected host was much higher in the Wisconsin area, ranging from 1 to 78 (average: 13), while in the Michigan area it ranged from 3 to 31 (average: 6) per infected host.

Dikmans (1940) described two North American species of *Nematospiroides*, bringing the number in the genus to 3. Unfortunately, our specimens do not agree with any of the described species. They appear to be nearest to *N. carolinensis* Dikmans, 1940, in that they possess a separate dorsal ray in the bursa, and have spicule lengths ranging from 1.9 to 2.4 mm. long in males which were 5.1 to 7.4 mm. in length. *Nematospiroides carolinensis* was described from *Clethrionomys* from North Carolina. No nematodes of this genus were found in any other hosts collected from the marsh where the heavy infections occurred in *Microtus*, although *N. longispiculatus* Dikmans, 1940, was found in both muskrats and voles collected in Washington, D. C., and in New Jersey (Dikmans, 1940).

Spurlock (1943) did some experimental work with the related species *Nematospiroides dubius* Baylis, which occurs as a parasite of house mice and other rodents. He found that some strains of laboratory mice were more susceptible than others, but was unable to draw any conclusions concerning acquired resistance. When large numbers of larvae were given, the mortality was high. The infection with this species of helminth apparently lasts for at least 8 months.

Spurlock also found that after the eggs of *Nematospiroides dubius* hatch, the free-living stage is passed in moist fecal material. The larvae are infective about 6 days after the deposition of the feces, and are found at that time on the surface of the fecal mass. Kirschenblatt (1938) has given further observations on the development of *Nematospiroides* larvae in *Microtus*.

Elton, Ford, and Baker (1931) studied the parasites of some European rodents, and found *Nematospiroides dubius* to be a common parasite of the

woodmouse, *Apodemus sylvaticus*, but did not find it in either *Clethrionomys* or *Microtus*. In 692 specimens of woodmouse, they found an incidence of infection of 85 per cent in adult animals. They also reported a high incidence during the summer and early autumn. The seasonal variation in incidence of infection with *N. dubius* was directly dependent upon age distribution of the animals, and, therefore, directly correlated with the breeding cycle. The question arises whether this is also true of the course of infection in *Microtus*.

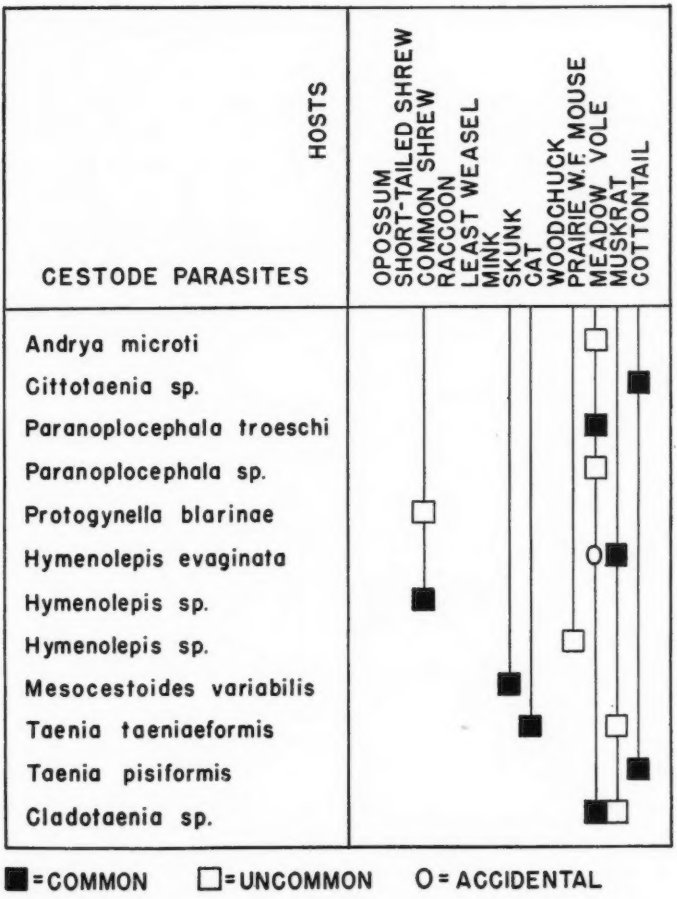

Fig. 4.—Host-parasite relationships on the Wisconsin study area. Part A. CESTODA.

Erickson (1944) reported that, in the snowshoe hare, *Lepus americanus* Erxleben, the helminth parasites are most abundant during the peak of the population cycle of the host. Elton, Ford, and Baker (1931) found that there was a higher percentage of woodmice infected by *Nematospiroides dubius* at the time of high density just before the mortality occurred, but no unusual increase in number of worms per infected animal.

Kirschenblatt (1938) found, with the same parasite, also in the woodmouse, that the number of worms ranged from 11 to 86, with an average of 34 per infected animal. He found larger infections in mountain forest areas than in open country, and considered the moist woods to be more suitable

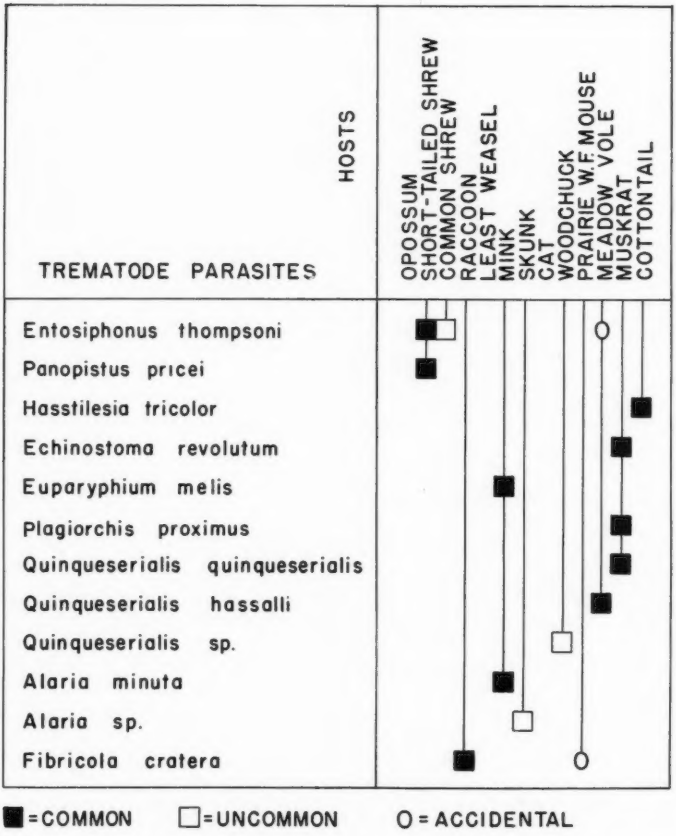

Fig. 4.—Host-parasite relationships on the Wisconsin study area. Part B. TREMATODA.

habitat for larval development. We observed heavier infections and a higher incidence of infection in the southern Wisconsin area, where the habitat was much wetter than in the Michigan area. Our observations seem to agree with those of Pearse (1930) in respect to the general relation of the helminths to the habitat of the host. It is of interest that we have never taken this nematode from animals of any species which were trapped within forest areas.

We have not yet examined enough infected voles to allow any observations on age susceptibility. Elton, Ford, and Baker (1931) showed, in the wood-mouse, that the infection with this nematode increases with the age of the host.

16. *Longistriata dalrymplei* Dikmans, 1935. (4).—Although it has been reported from several localities (Dikmans, 1935), this nematode was found to be uncommon in the voles of the region considered here. Infected animals were taken only at Horicon Marsh, Wisconsin, from *Microtus p. pennsylvanicus*. Other foci of infection may occur in the region studied, but, if so, they were overlooked because of the relatively small number of animals examined.

The life cycle of a related species, *Longistriata musculi* Dikmans, 1935, has been studied by Schwartz and Alicata (1935), and it was found that larvae may gain entrance to the host either by way of ingestion or through the skin.

It seems probable that voles can withstand fairly heavy infections with this parasite, without serious result. The infections we observed were medium; the maximum number of worms seen in a single host was 48.

17. *Dictyocaulus viviparus* (Bloch, 1782). (17).—Two males and a single female, the latter containing many embryonated eggs, were recovered by one of us (R. R.), apparently from the cecum of a vole from southern Michigan. Before the worms were fixed, the absence of a separate dorsal lobe in the bursa and the heavy spicules of the males were noted. The problem of identification was transmitted to the junior author. The finding of bursate strongyloid worms in the intestinal tract suggested that they belonged to the family Trichostrongylidae Leiper, 1912. Detailed drawings were made, and a search through the literature was undertaken in an effort to determine their systematic position. This proved to be quite without result until similarity was noticed between the dorsal rays of the bursa in our drawings and those of Dikmans (1936; Fig. 1, No. 11). A subsequent comparison of our specimens with *D. viviparus* from domestic cattle indicated that they belonged to this species. Our material was then sent to Dr. Dikmans, who replied that he could only confirm the identification.

Both Dr. Dikmans and Dr. G. R. LaRue cautioned the authors that contaminated equipment or faulty labeling might have been a source of error. However, cattle were not autopsied in the same building where the voles were examined, and petri dishes used by us were used in addition only for bacteriological purposes. The fact that the worms were studied while still alive seems to preclude any possibility of faulty labeling. We had no doubts as to their source while in the process of identifying them. We feel obliged to as-

sume, therefore, that the worms actually were present in the intestinal tract of the vole.

It would seem that the vole had ingested the worms as larvae, and that

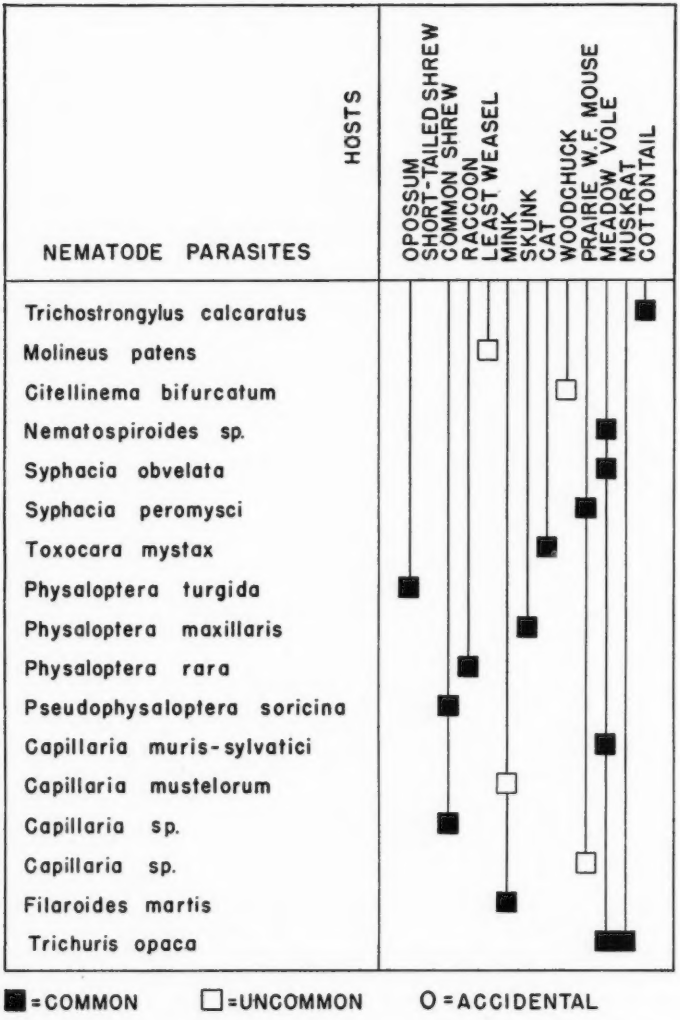

Fig. 4.—Host-parasite relationships on the Wisconsin study area. Part C. NEMATODA.

they had grown to maturity in its cecum. Since voles reduce their food to rather small size before it reaches the stomach, it does not seem likely that such large worms could have been ingested intact. Beef cattle were pastured in the same field where the vole was collected. We do not know if these animals were infected with *Dictyocaulus viviparus*.

It is of interest that Dougherty (1946) has decided that there is morphological evidence for classifying the genus *Dictyocaulus* in the Trichostrongylidae.

OXYURIDAE

18. *Syphacia obvelata* (Rudolphi, 1802). (1, 2, 3, 4, 5, 7, 8, 12, 13, 15, 16, 17, 18, 20, 21, 22).—The most common helminth encountered in the voles of this region, *S. obvelata* was widely distributed. It was also recorded from *Microtus pennsylvanicus drummondii*, from near Winnipeg, Manitoba, and was observed in the house rat in Michigan, Ohio, and Wisconsin, and in the house mouse in Illinois.

The life cycle of this nematode is direct (Lawler, 1939), and there does not appear to be any immunity developed, age or otherwise, according to what has been learned from work with other rodents (Culbertson, 1941; Taliaferro, 1929).

Syphacia obvelata was found throughout the year. On the southern Michigan study area, it was found, during the first summer, that relatively few animals were infected, but the average number of worms was high. Later, during the winter, a large proportion of the population was infected, but with a lower average number of worms per infected animal. Of the 345 voles collected from this area, 30 per cent were infected with this parasite. The average number of worms per infected animal was 15.5, with a maximum number of 242 worms occurring in a single host. On the Wisconsin area, where the habitat was much wetter, 30 per cent of the animals also were infected. In this latter area, *Syphacia peromysci* Harkema, 1936, occurred commonly, and apparently was parasitic only in *Peromyscus* spp.

Kirschenblatt (1938; graph 12, page 36) found the peak of infection during the spring, in *Microtus*, with the maximum average number of worms per animal at this time, also. He observed two peaks of infection, one in the spring and one in the fall, in *Mus musculus* subsp. *Syphacia stroma* (von Linstow, 1884) showed, in the woodmouse, a behavior similar to that of *S. obvelata* in *M. musculus* subsp.

Male worms were rare, a condition previously noted by other workers (Hall, 1916), but in a few cases a majority of worms was males. Kirschenblatt (1938; page 36) stated "I found males more than once, and furthermore in some cases the number of males exceeded the number of females. Frequently it happened that the males were not found in the presence of females. The males of *S. obvelata* do not appear to be a rarity, as it seems that one would judge from the data of Linstow, Hall, and Schultz. But evidently they live a considerably shorter period than the females. It was impossible to establish any rule as to the relationship of the number of males to the females in the various seasons of the year. The absence of males seems especially strange in the comparatively large material that Schulz had. One

cannot escape the thought that the males as a result of their small size were lost in the washing of the gut with water, according to the method of helminthological investigation of Skrjabin, or they burst in the water and were useless for further systematic study."

SPIRURIDAE

19. *Mastophorus muris* (Gmelin, 1790). (17).—An uncommon parasite of voles of this region, *Mastophorus muris* (=*Protospirura muris*; see Chitwood, 1938) was found only in southern Michigan, and occurred in only 2 per cent of the 345 animals examined from this study area. This helminth was collected during the winter, spring, and summer of 1946. According to Hall (1916) after Leuckart (1867) and Marchi (1871), the eggs of *M. muris* are ingested by beetles of the genus *Tenebrio*, and in five weeks encapsulated larvae are found in the body cavity. Baylis (1931) stated that meal beetles and a cockroach, *Blatella germanica* (L.), probably act as the intermediate hosts for *M. muris* near human habitations, but that other insects probably replace them in more remote areas. Whether or not voles purposely ingest such insects is not definitely known.

Kirschenblatt (1938) stated the length of life of these worms is comparatively long, apparently not less than a year, and that the number of worms does not depend upon definite seasons.

In the few voles infected with this parasite, no evidence of any pathogenicity was observed, since neither local lesions nor deteriorated physical condition of the host were evident. Lesions such as those caused by *Physaloptera* spp. in some of their respective hosts were in no case evident in the stomachs of the infected animals. The heaviest infection, with 17 large female and 3 male worms, was observed in a female vole. This animal, collected on July 21, 1946, weighed 63 grams, and contained 9 nearly full-term fetuses. The average number of worms, for the five infected animals, was 7.

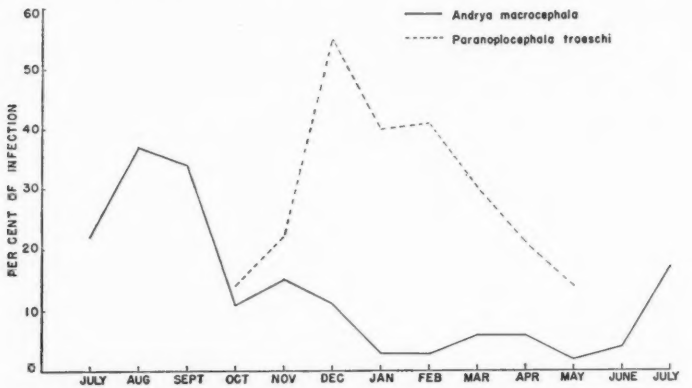

Fig. 5.—Seasonal variation in *Andrya macrocephala* and *Paranoplocephala troeschi* infections in voles. Based on 345 voles examined from the Michigan study area.

TRICHURIDAE

20. *Capillaria muris-sylvatici* (Diesing, 1851). (5).—We know little so far about this nematode, which was recorded from a single area in Wisconsin. We are indebted to Mr. Clark P. Reed, Rice Institute, for the identification of nematodes of the genus *Capillaria*. This species was not recorded from hosts other than voles.

Although accurate counts were difficult, infections with *Capillaria muris-sylvatici* apparently consisted of up to about 40 worms. The data given by Kirschenblatt (1938) on members of the genus *Capillaria* from Russian rodents might be mentioned here. He gave information on *C. hepatica* Bancroft, 1893, in the snow-mouse, *Chionomys nivalis* Mart., and on *C. gastrica* Baylis, 1926, in *Microtus socialis*. He stated (page 30) that "young infected specimens (of *Microtus*) weighing from 21 to 27 grams were found only in February; in the rest of the year only old infected animals were encountered. Evidently the duration of the life of the worm is great, therefore the extensiveness of the infection increases with age." The same author observed a similar behavior of *C. hepatica* in *Chionomys* (graph 8, page 28).

21. *Trichuris opaca* Barker and Noyes, 1915. (5, 18).—Whipworms which belonged to this species were collected from both the vole and the

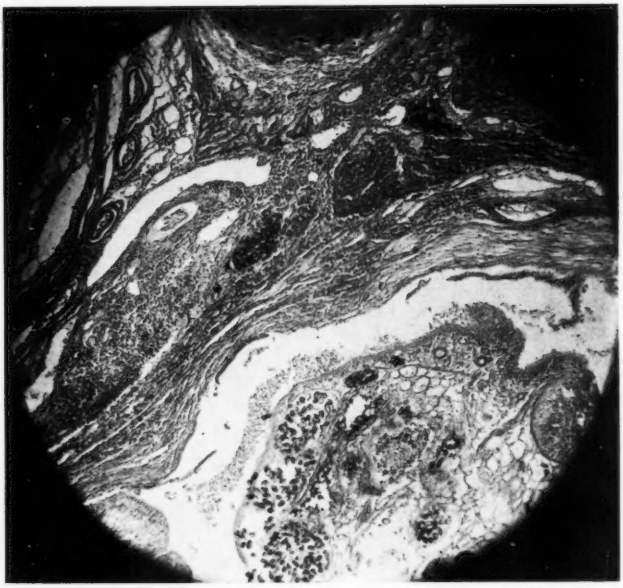

Fig. 6.—Photomicrograph of a liver section from a vole infected with *Mediogonimus ovilacus*. ×70.

muskrat from the southern Wisconsin marsh area, and from a vole from southern Michigan. Of the animals examined, the voles harbored a larger number of worms per infected animal than did the muskrats; however, a much larger number of voles was examined. Of the 43 voles from the marsh area, 11 were infected, while 4 of the 6 muskrats examined were infected. Infections in the former host ranged from 1 to 26 (average: 9.6) per infected animal, while in the muskrat infections ranged from 2 to 12 (average: 4.6) per infected animal.

Records of *Trichuris* from the muskrat do not appear to be numerous. Dr. E. W. Price informed us that the U. S. National Museum Helminthological Collection has only a single vial of whipworms from the muskrat, collected in Maryland. It appears to us that the vole may be a more important host for *T. opaca* than is the muskrat.

Hall (1916) has pointed out that there is a discrepancy between the measurements in Barker's drawings and text. Through the courtesy of Dr. H. W. Manter, University of Nebraska, type specimens of *Trichuris opaca* were made available to the writers. Figures 1 and 3 are essentially correct, and are drawn to the same scale, although the cloacal tube of the male in Figure 1 was confused with the spicule. No specimens could be found which corresponded to Figure 2, but it shows more accurately than Figure 1 the details of the posterior end of the male, provided that the scale (Figure 2) is changed to read approximately ".37 mm." The spicule length given in the text should be corrected to read "1.35 mm." Additional work will be necessary to adequately redescribe *T. opaca,* and to determine its affinities with other species of *Trichuris* from rodents.

22. *Trichuris* sp. (9, 11).—In addition to the aforementioned *T. opaca,* females of a *Trichuris* sp. were collected from *Microtus ochrogaster* in Illinois. The absence of male specimens prevented our determining their specific identity.

DISCUSSION AND CONCLUSIONS

From the foregoing material, it is evident that much is yet to be learned concerning the helminths parasitic in voles, to say nothing of the parasites of wildlife in general. However, only long-term studies can make substantial contributions toward solutions of the basic problems involved. At present, nothing definite can be said concerning the effect of helminth parasites on population fluctuations of rodents.

During the course of our work we have not been able to observe any definite connection between population density of voles and parasite density. Both quantitative and qualitative differences in helminth infections appear to be seasonal or geographical in nature. This opinion is sustained by the previous work on the helminths of sciurids (Rausch and Tiner, 1948).

One is much impressed by the localized nature of infections with certain helminths over the North Central States region. This is especially marked in the case of certain vole parasites, such as *Trichuris opaca, Mastophorus muris, Capillaria-muris sylvatici, Longistriata dalrymplei,* and *Mediogonimus*

ovilacus. This phenomenon was pointed out by Kirschenblatt (1938), and was stated as follows in his summary: "Dabei hatte es sich erwiesen, dass die Invasion der mäuseähnlichen Nagetiere mit Parasiten nicht nur in verschiedenen Ortschaften eine verschiedene ist, sondern sich auch in verschiedenen Kolonien in ein und derselben Ortschaft unterscheidet. Die Unterschiede in der Invasion der Nagetiere aus einer Kolonie werden im Allgemeinen durch die Altersunterschiede verursacht und hängen von der Jahreszeit ab." He stated further that: "Die Helminthen-fauna der mäuseähnlichen Nagetiere in der Umgebung von Tbilisi ist im Frühling (Mai) am reichsten und am verschiedenartigsten, im Sommer (Juli) dagegen am ärmsten und am wenigsten verschiedenartig. Sommerhitze und Trockenheit hemmen die Invasion der Nagetiere mit den meisten Helminthen-Arten. Deshalb stellt der Sommer in den Steppen Transkaukasiens eine solche Jahreszeit dar, während welcher die Nagetiere sich spontan von den meisten Helminthen befreien."

The occurrence of *Nematospiroides* sp., *Trichuris opaca*, and *Capillaria muris-sylvatici* in the isolated marsh in southern Wisconsin, and their apparent rarity in the surrounding areas, may be evidence of environmental influence. The importance of habitat in the case of certain other helminths is self-evident. As has been noted by other writers, anoplocephaline cestodes occur most abundantly in animals from areas suitable to free-living mites; the heaviest infections being observed in animals from areas with heavy stands of grass.

With the exception of *Mediogonimus ovilacus*, we were unable to determine that the helminths parasitic in voles had any deleterious effect upon the host. Evidence seems to substantiate results obtained from the study of sciurid helminths (Rausch and Tiner, 1948)—i.e. many helminths probably can be considered innocuous when the host is living in its natural state; many of these should possibly be considered more nearly commensals than parasites.

It was noted that there was a greater number and variety of helminths present in the northwestern part of the region considered, with fewer in the eastern and southern parts. This was also observed in the case of the sciurid parasites. It may be that drainage and heavy cultivation of the southeastern part of the region has exerted considerable influence on some of the vole parasites, which appear to require a fairly wet habitat. However, the number of hosts so far examined is hardly large enough to allow any conclusions concerning helminth distribution.

Not only can new host- and new distribution records be obtained from nearly every area where intensive studies are made, but new species are also often found, indicating that our knowledge of the North American helminth fauna is still quite incomplete. Especially is little known of the epizootology of helminths parasitic in wild birds and mammals, and in connection with this, there is much opportunity to make valuable observations on the basis of season-to-season studies.

SUMMARY

A total of 648 voles of three species, collected since 1942 from the states of Ohio, Indiana, Illinois, Michigan, Wisconsin, and from Manitoba, has been examined for helminth parasites. Special reference has been made to host-

parasite relationships, and detailed information has been given for two areas where intensive studies were made.

A total of 21 species of helminths was collected, some of which are recorded from voles for the first time. The helminth species encountered have been discussed separately in the text.

Information has been given on seasonal variation in infections with certain helmiths. There is evidence that season of the year and geographical location have much influence on kind and number of helminths parasitic in voles. As far as we have been able to determine, most of these vole parasites have little or no harmful effect upon the host.

TABLE I.—Summary of Results.

Host	No. examined	Parasite	No. infected
Microtus p. pennsylvanicus	570	*Andrya macrocephala*	59
		Andrya microti	1
		Andrya sp.	4
		Paranoplocephala troeschi	90
		Paranoplocephala spp.	32
		Hymenolepis fraterna	1
		Hymenolepis evaginata	2
		Taenia taeniaeformis	43
		Cladotaenia spp.	13
		Quinqueserialis hassalli	21
		Mediogonimus ovilacus	2
		Entosiphonus thompsoni	3
		Nematospiroides sp.	32
		Longistriata dalrymplei	3
		Dictyocaulus viviparus	1
		Syphacia obvelata	145
		Mastophorus muris	6
		Capillaria muris-sylvatici	18
		Trichuris opaca	11
Microtus p. drummondii	32	*Andrya macrocephala*	1
		Taenia sp.	1
		Syphacia obvelata	3
Microtus ochrogaster	46	*Andrya macrocephala*	5
		Paranoplocephala sp.	9
		Choanotaenia sp.	1
		Hymenolepis sp.	1
		Taenia taeniaeformis	1
		Cladotaenia sp.	1
		Quinqueserialis hassalli	1
		Syphacia obvelata	13
		Trichuris sp.	2

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Dr. Louise A. Scherger, Mr. Felix Hartmeister, and Mr. Lloyd Otteson have given much technical assistance. Dr. Banner Bill Morgan and Mr. C. P. Read have very kindly identified certain of the nematodes encountered.

The senior author feels deeply indebted to the late Professor Aldo Leopold for many valuable suggestions and encouragement in connection with these investigations.

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On the Occurrence of Algal Remains in the Ancient Rocks of Angola*

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The existence of algal remains in the older African formations was first recognized by A. Salée (1) who, in 1931, at the Kigoma meeting of the African Geological Surveys Association, announced his discovery of stromatolites in rocks of the Lumpungu System of Rwanda-Urundi and the Malagarasi

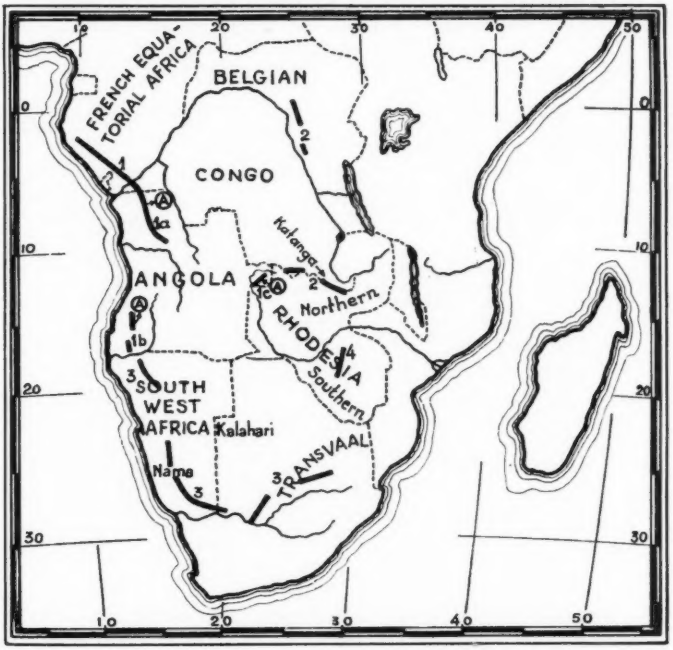

Fig. 1. Geographic distribution of equivalent systems.—1. Congo Occidental System, Belgian Congo and French Equatorial Africa. 1a. Bembe System; Northwest Angola—Portuguese Congo. 1b. Bembe System; Southwest Angola—Humpata, Chela. 1c. Bembe System; Eastern Angola—Alto Zambese. 2. Katanga System; Belgian Congo, Katanga. 3. Nama–Transvaal Systems, South West Africa and the Transvaal. 4. Lomagundi System; Southern Rhodesia. A—Algal occurrences in Angola.

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Series of Tanganyika. This discovery was substantiated by J. Schuster (2) and W. Dietrich (3), who examined the finds and pronounced them to be true algal structures, of a kind ranging in age from Pre-Cambrian to early Paleozoic.

Following upon these discoveries, an ever-increasing number of observers drew attention to similar occurrences in many different African localities and showed that the older rocks of the continent contain a wealth of material, consisting either of the actual remains of the algae themselves or of structures formed by them in symbiotic association with bacteria or other lowly organisms, by precipitation of calcareous matter or agglomeration of sediment.

Of the many contributions to this work, those of R. B. Young (4) are outstanding for his clear exposition of the nature of stromatolites and of the processes involved in their formation. It is based on a study of those found in the dolomites of South-West Africa. Young conclusively showed that a parallel could be drawn between these ancient structures and those of recent formation studied by M. Black (5) at Andros Island in the Bahamas. Great credit must be given also to C. M. Schwellnus and H. D. Le Roex (6), who, following a study of certain forms contained in the Otavi Dolomite, emphasized their origin through "the action of organic agents such as algae."

Early in 1940 A. M. Macgregor (7) of the Southern Rhodesia Geological Survey recorded the occurrence of algal structures in a graphitic concretionary limestone forming part of the Pre-Cambrian sequence of Southern Rhodesia.

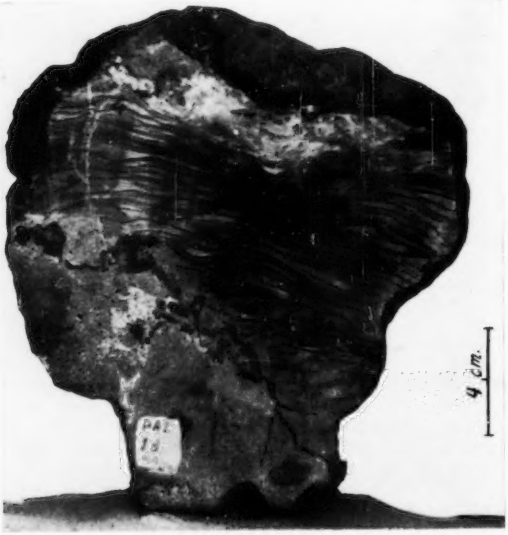


Fig. 2.—Concave, laminated growth overlying limestone, which is seen in the lower part of the specimen. Northwest Angola. (This specimen bears considerable resemblance to *Collenia symmetrica* F. & F. of the Belt Series in Montana and Alberta.)

In 1944 A. Jamotte (8) identified the cauliflower-like structures found in the Ruashi Mine of Katanga, in the Belgian Congo, as those of limestone-building algae belonging to the genera *Collenia* and *Cryptozoon*. Subsequent discoveries made in the Belgian Congo by many workers, including L. Cahen, G. Mortelmans, J. Lepersonne (9), F. Sluys (10), A. L. Hacquaert (11) and E. Pollinard (12), revealed the widespread occurrence of algal forms in the older rocks of that territory, while certain structures described by Babet (13), and considered by Jamotte to be those of an alga of *Collenia* type, extended their known range into French Equatorial Africa. Their distribution farther afield has been shown by the discoveries of G. Choubert (14) in the Atlas; of R. Furon (15) in Nigeria; and of Menchikoff (16) in the Western Sahara. To these discoveries may now be added those made by the writer in Angola in and since 1945.

It is not my purpose to give a full history of the discovery of algal fossils in Africa, but rather to draw attention to their occurrence in Angola. A complete bibliography of the subject is given by Menchikoff in the paper referred to above. It is sufficient here to say that steady progress has been made in this field during recent years, springing from the work of many observers and emphasizing how wide is the distribution of *Collenia* and its related forms in the rocks of Africa. The writer has been primarily concerned with the value of these fossils as stratigraphical indices, and the aid they may afford in locating key horizons in Angola—horizons which can be correlated with those of neighboring territories.

Fig. 3.—Concentric silicified growths, Northwest Angola. (These almost certainly are referable to *Collenia*, perhaps of the *C. Willisii* type.)

The algal remains of Angola occur in rocks of the so-called Bembe System, a group of ancient formations that rest with a pronounced unconformity upon older Systems. The Bembe System, which derives its name from a locality well known for its copper workings, outcrops in three independent and widely separated areas: Portuguese Congo, in the northwest; Alto Zambeze, in the east; and Humpata-Chela in the southwest.

The Portuguese Congo exposure is part of a long belt that stretches in a general southeasterly direction from the French territory of Gaboon to the vicinity of the Cuanza River. The Alto Zambeze exposure is a small portion of a belt that passes through Katanga and Northern Rhodesia, while the Humpata-Chela exposure is doubtless the northern continuation of the Nama System of South-West Africa.

The discovery of algal remains in the Bembe System brings it into palaeontological line with the corresponding systems established in neighboring territory, and makes possible a more precise correlation than that based only on lithological characters and structural relationships, as was previously the case. But before discussing the implications of the algal finds, however, it will be advantageous to consider briefly the classification adopted for the Bembe System and to compare its component stages with those recognized in the equivalent systems of the Belgian Congo and elsewhere. This is the more desirable since the subject is beset by a confused and overlapping nomenclature that has grown out of the necessity (due to the absence of palaeontological evidence) of giving local definitions to the rocks of separated areas.

The Bembe System as developed in the northwest of Angola fully corresponds with the Congo Occidental System established in the adjacent territory of the Belgian Congo. In both areas there is a thick basal tillite succeeded by a Lower Series (Série Schisto-Calcaire of the Belgian geologists) which is predominantly calcareous in nature, and an Upper Series (Série Schisto-Gréseuse of the Belgian geologists), which is predominantly arenaceous and probably is of continental origin. These series are separated by a considerable

Fig. 4.—Massive, non-silicified algae with fingerlike outgrowths. Northwest Angola.

hiatus and at the base of the Upper Series there occur breccias (Luidi Breccia of Angola; Bangu and Niari Breccias of the Belgian Congo and French Equatorial Africa) which probably are tillites. The lithological characters and constancy of facies of the Angola rocks repeat in a striking manner those recognized in the Bas-Congo by Delhaye and Sluys (17). The Upper Series has been recently correlated with the topmost beds of the Kundelungu Series of Katanga (18), so that the great hiatus that separates it from the Lower Series corresponds in time with the deposition of the greater part of the Kundelungu rocks.

The writer's recent work in the Alto Zambeze area has shown the succession to be more complete than was formerly supposed, and has permitted closer comparison of the rocks with those of Katanga and Northern Rhodesia. However, the geology of the area still is very imperfectly known, for outcrops are scarce because older formations are concealed under a thick covering of surface sand. Nevertheless, a correlation can be made with the Katanga succession. Thus the group of sandstones and quartzites that form the basal part of the sequence are comparable with the Lower Roan Series, while the overlying shales and dolomites correspond to the Upper Roan Series (Mine Series). These rocks are succeeded by carbonaceous shales similar to those of the Mwashya Series, which is partly of glacial origin. Next comes, as in Katanga, a tillite, well known as the "Grand Conglomérat du Kundelungu." Above this the Alto Zambeze succession is incomplete; so far as is known, the upper portion of the Katanga System is entirely missing, the highest beds exposed corresponding to the lowest part only of the Kundelungu Series, a state of affairs presumably due to uplift and erosion.

In the Humpata-Chela area, the upper part of the system is again missing and no formations of Kundelungu age are known, perhaps because of the intense erosion which this country has suffered. There is a basal tillite, known only in the extreme south, and the succeeding beds consist of sandstones and

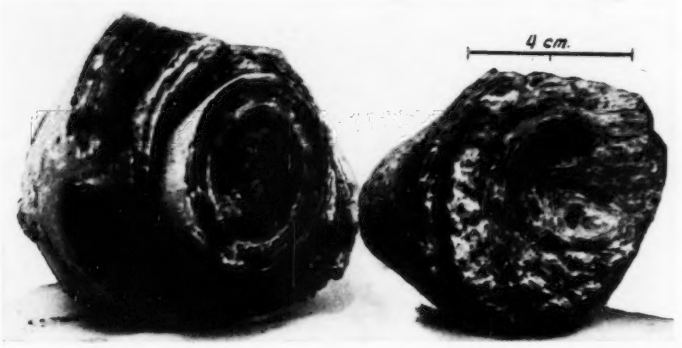
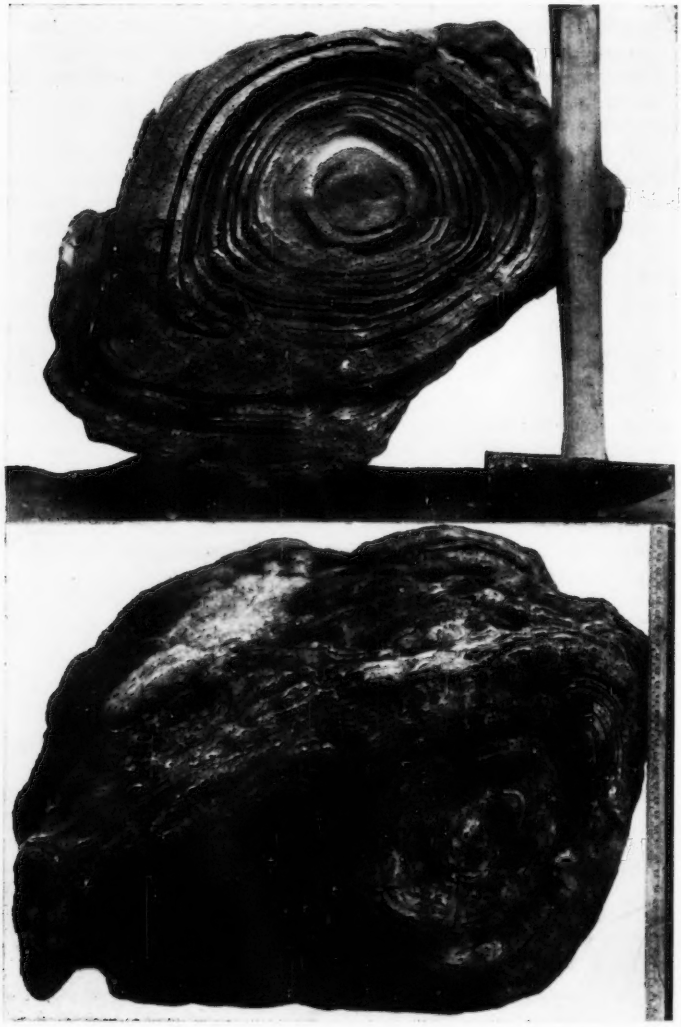


Fig. 5.—Conical silicified forms. Northwest Angola. (These resemble the conical ecad of *Collenia frequens* Walcott of the Belt.)

quartzites. Above these lie dolomites which correspond to those of Otavi in the adjacent territory of South-West Africa. The overlying Fish River Beds of that territory are not represented.



Figs. 6, 7.—Forms showing concentric laminae surrounding apparently solid nuclei. Alto Zambeze.

TABLE 1.—Comparison of the Bembe System and related Pre-Cambrian "systems" of southern Africa.

Congo Occidental System (Bembe Syst.)			Bembe System	Katanga System	Bembe System	Nama System
N. W. Angola (Congo Occ.)	Belgian Congo (Occ.)	French Equat. Africa (S. W.)	E. Angola (Alto Zambeze)	Belgian Congo (Katanga)	S. W. Angola	S. W. Africa
"Schisto-Gréseuse" Series			?	Upper Kundelungu Series "Petit Conglom." (Tillite)	?	Fish River beds
Luidi, Bangu-Niari congl. & breccia			(pars) Lower Kundelungu Series "Grand Conglomérat" (Tillite)			
(*Algae*) "Schisto-Calcaire" Series			Mwashya Series (*Algae*) Mine Series (Upper Roan Series)		(*Algae*) Humpata dolomit. limestone	(*Algae*) Otavi Dolomite
Bembe, Bas-Congo Tillite			Lower Roan Series		Chela shales & sandst. Tjamalindi Tillite	Kuibis basal beds Numees Tillite

It has long been supposed—a supposition strongly supported in the writings of M. Robert (19), P. Fourmarier (20), H. Lagotala (21) and A. Jamotte (9)—that the detached outcrops of these ancient formations of Central Africa, which form two broken ring-like belts around the Congo and Kalahari depressions and are linked in Angola, as shown in the accompanying map, were contemporaneous or at least penecontemporaneous in origin. This view, once based upon identity of lithology and structure, has received confirmation from the discovery of algal fossils. Jamotte first applied this knowledge to the correlation of these African formations. In 1941 he framed a correlation based on this method, and although he could not then extend it to Angola, Jamotte suggested that the rocks of this territory were not to be excluded, an opinion that has since been fully vindicated.

The first of the algal fossils discovered in Angola came from the Bembe area of the Portuguese Congo, at the Mavoio River. Here, at the top of the limestone and immediately underlying an argillaceous horizon with cherty intercalations, occurs a well-marked silicified band consisting of black pseudo-ooliths set in a white matrix. The rock has a striking aspect and is readily recognized. At a meeting of Belgian, French and Portuguese geologists held at Leopoldville in 1945 (18), the writer ascertained that this rock agrees precisely, both in macroscopic and microscopic features, with that characteristic of the "Kisantu Level" (Stage C4) of the Belgian succession of "Série Schisto-Calcaire," and in which A. L. Hacquaert (11) had recognized forms which he regarded as those of *Schizophyceae* (*Porostromata* of M. H. Pia).

Field work during 1946 and 1947 showed this "oolitic level" to have a

Fig. 8.—A silicified, undulose and conspicuously laminated alga resting upon edgewise breccia. Southwest Angola. (This fossil closely resembles the laminar-expanded ecad of *Collenia versiformis* F. & F. of the northern Belt Series. The habit of growing upon edgewise breccia is common in *Collenia* and *Cryptozoon*.)

remarkable persistence, thus providing an important key-horizon of the Bembe System. Moreover, it was found to contain a wealth of stromatolitic forms, together with others that may be classed for the present as *incertae sedis,* though in their mode of occurrence they strongly suggest an organic origin. The stromatolites apparently belong to the form-genus *Collenia,* and range from types resembling *C. undosa,* Walcott to more complex forms. A form resembling *Conophyton* was found early in the year 1948 by J. Trigo de Mira in the southern extremity of the belt, near Quiongua.

The dolomites of the Humpata-Chela area have also yielded some interesting material, one specimen being a fine example of a colonial growth of branching columns. The writer has had the opportunity of making only a hurried examination of this area, but he anticipates that material more like that occurring in the Otavi Dolomite will be found here.

In the Alto Zambeze area there occurs a somewhat peculiar red and ferruginous rock whose origin is obscure but which is probably a highly altered and silicified dolomite. It contains orbicular structures (fig. 5) which appear to be similar to those described by E. Polinard (12). These structures are remarkable for their constant repetition and are found wherever the rock outcrops.

Of particular interest was the discovery in 1947, on the south bank of the Niela River, of silicified structures definitely referable to *Collenia,* since this find confirmed the existence in Alto Zambeze of the Mines Series of Katanga, previously postulated on lithological grounds by Belgian geologists working in the area some years ago. The rock in which these fossils occur is completely silicified, but was doubtless originally a somewhat sandy dolomite. It corresponds well with the "roches silicieuses cellulaires" of Katanga. Furthermore, the discovery in the same year of an oolitic rock resembling that of Kisantu so closely as to be indistinguishable from it in hand specimens, and occurring in proximity to carbonaceous shales, threw further light on Alto Zambeze stratigraphy for it showed conclusively that the topmost beds of Mine Series as well as Mwashya Series are well represented here. It was in a similar oolitic rock from Katanga that A. L. Hacquaert recognized *Girvanella Robertii.*

The significance of these finds, which fill gaps in previous knowledge of Angolan stratigraphy, has constrained the writer to put them on record here, although he is not competent to undertake a specific determination of the fossils. That task must be left to a specialist. But their very occurrence has served to bring the Bembe System into harmony with those recognized in neighboring territories, and has placed it in definite relationship with the formations of Central Africa. Moreover, these algal remains, either of themselves or considered in relation to the peculiarities of their environment, make it possible to recognize the existence of particular horizons and to correlate the somewhat contrasted facies of three different areas in which the Bembe System occurs.

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The Teloschistaceae of Wisconsin

Papers on Wisconsin Lichens. III.

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Two preceding papers in a series of studies on the lichen flora of Wisconsin have already been published. They are upon *Cladonia* (Amer. Midl. Nat. 27: 696-709. 1942) and *Peltigera* (Trans. Wis. Acad. 38: 249-272. 1947). Attention was brought to the Xanthorias by their abundance and widespread occurrence in this state. Excellent treatments of the Teloschistaceae by Hillman made the preparation of a treatment of the Wisconsin species comparatively easy.

The Teloschistaceae are yellow foliose or fruticose lichens with a thalloid exciple. The spores are eight in the ascus and are polar two-celled. Usually, as in the present paper, the foliose and fruticose species are placed in separate genera, but Fink and Tuckerman included both in one all-inclusive genus, *Teloschistes*.

Some other yellow lichens at times give trouble in determinations: *Candelaria concolor* very closely resembles *Xanthoria concolor* but, as later pointed out, can be distinguished by KOH reaction as well as by the larger number of spores in the ascus. *Caloplaca elegans* may also give some trouble, but the center is crustose and only the outer lobes of the thallus are more or less foliose. According to Annie L. Smith the yellow color in *Xanthoria* and *Caloplaca* is due to parietin, a yellow lichen acid which gives a reddish-purple reaction with KOH; in *Candelaria* the yellow acid is stictaurin which gives no reaction with KOH.

In Wisconsin, the Teloschistaceae are primarily found on bark, only occasionally on rocks. Deciduous trees, especially poplars, elms, and maples are preferred habitats, although fence posts may also be covered. At times the bases of the elms lining the highways in the prairie and oak-hickory forest regions are yellow. *Xanthoria fallax* is the most common species in these regions, *X. polycarpa* being more abundant on the aspens of the cut-over northwoods, and *Candelaria concolor* of the Lecanoraceae being very abundant on the oaks of the jack pine-scrub oak association. Sometimes it is noticed that the Teloschistaceae are more abundant on the elms near farms and farm yards. There seems a possibility that the richer, manure-containing dust of such places may promote more luxuriant growth of the Xanthorias. Are they, like the Caloplacaceae, essentially nitrophilous as Lynge has suggested for that family?

Unless otherwise stated the cited specimens were collected by the writer. Additional specimens have been generously collected by Drs. R. I. Evans and N. C. Fassett. All specimens are in the herbarium of the University of Wisconsin.

KEY TO THE WISCONSIN TELOSCHISTACEAE

1. Thallus foliose, rhizinae present on the underside—(*Xanthoria*).
  2. Lacking soredia, apothecia usually abundant.
    3. Thallus usually several cm. in diameter, lobes up to 5 mm. broad, flat to slightly convex toward the margins .....[1. *X. parietina*]
    3. Thallus usually smaller, forming small rosettes up to 2 cm. in diameter; lobes narrow, about 0.5 mm. broad, strongly convex, frequently completely covered by the numerous apothecia.
      4. Thallus yellow to orange-red, KOH + red .....2. *X. polycarpa*
      4. Thallus greenish-yellow, KOH minus .....2a. *X. polycarpa* f. *chlorina*
  2. Sorediate or isidiate, apothecia infrequent.
    5. Thallus lobes narrow, more or less linear, apices tending to be isidia-like; soredia infrequent and scattered along the margins .....3. *X. candelaria*
    6. Thallus of lobes with short isidiform apices .....3a. *X. candelaria* var. *finmarkica*
    6. Thallus almost entirely converted into masses of soredia .....3b. *X. candelaria* var. *leprosa*
    5. Thallus lobes slightly broader and shorter, apices rounded, not isidiform, granular soredia usually abundant in soralia on the underside of the sides and at the tips of the lobes.
      7. Thallus golden to orange-yellow .....4. *X. fallax*
      7. Thallus greenish or grayish yellow .....4a. *X. fallax* f. *chlorina*
1. Thallus fruticose, underside lacking rhiziniae but lobe margins and exciple with pale whitish ciliae .....5. *Teloschistes chrysophthalmus*

[1. *Xanthoria parietina* (L.) Th. Fr. Lich. Arct. 67. 1860]

Lichen parietinus L. Spec. Plant. 1143. 1753. *Parmelia parietina* Schaer. Enum. Crit. 49. 1850. *Teloschistes parietinus* Norm. Nyt. Mag. Naturv. 7: 229. 1853. *Physcia parietina* Koerb. Syst. Lich. Germ. 91. 1855.

Thallus foliose, up to 20 cm. broad, more or less closely appressed, greenish yellow or more usually golden yellow or orange-red. Lobes 1-5 mm. broad, smooth or occasionally roughened, lacking soredia, not shining, tips rounded. Underside whitish with sparse whitish rhizinae. Apothecia adnate to sessile, concave to flat, rounded, up to 5 mm. broad, the disk orange. Exciple thick, concolorous with the thallus, smooth to occasionally crenate or isidioid. Hymenium and hypothecium hyaline. Spores two-celled, polar, hyaline, ellipsoid 10-18 x 6-10 μ. Thallus and apothecia KOH+, purplish-red.

Although the range in Fink's "Flora" is given as northern United States and California, *Xanthoria parietina* appears to be primarily maritime, being more common near the Atlantic Coast. Apparently it is not as abundant in this country as in Europe where it is the most common of the Xanthorias. Tuckerman gives the range a little better, citing the Atlantic seaboard and then "shores of Lake Superior, Agassiz." Papers by Hedrick and by Darlington on Northern Michigan, by Hedrick and Lowe on Isle Royale, and by Fink on Minnesota do not report this species although Fink lists it from Wisconsin in *Notes on Lichen Distribution in the Upper Mississippi Valley*. Macoun reported collecting it on stones along Lake Winnipegosis, Manitoba.

Further south it is reported from Ohio by Wolfe and from Indiana by Herre. Although there is a possibility that it may occur in Wisconsin, I have not as yet located authentic material, and have not seen it on either the north or south shores of Lake Superior. Specimens in the author's exsiccatae of Wisconsin Lichens distributed under this name (No. 12) have turned out to be *X. fallax* as very kindly determined for me by Dr. G. Degelius. Specimens to confirm the existence of this species in Wisconsin should be sought.

2. *Xanthoria polycarpa* (Ehrh.) Rieber, Jahres, Ver. Vaterl. Naturk. Württ, 47: 252. 1891.

Lichen polycarpus Ehrh. Plant. Crypt. Exs. No. 136. 1789. *Lobaria polycarpa* Hoffm. Deuts. Flora 159. 1795. *Parmelia polycarpa* Hepp. Würzb. Lich. Flora 39. 1824. *Physcia polycarpa* Kieffer Hedwigia 33: 114. 1894. *Teloschistes polycarpus* Tuck. Syn. N. A. Lich. 1: 50. 1882. *Parmelia parietina* var. *polycarpa* E. Fr. Lich. Eur. Ref. 73. 1831. *Physcia parietina* var. *polycarpa* Krplhb. Denkchr. K. Bayer. Bot. Ges. Regensb. 42, 141. 1861. *Physcia parietina* f. *polycarpa* Rieb. Flecht.-Flora Umgeb. Ehingen 14. 1901. *Xanthoria parietina* var. *polycarpa* Rabh. Krypt.-Flora Sachsen 281. 1870. *Xanthoria parietina* f. *polycarpa* Arn. Lichen-Flora München 2: 12. 1897. *Xanthoria lychnea* var. *polycarpa* Sydow Flecht. Deuts. 52. 1887. *Parmelia parietina* var. *leptophylla* Wallr. Flora Crypt. Germ. 1: 515. 1831. *Physcia parietina* var. *pulvinata* Mass. Sched. Crit. 42. 1856.

Thallus foliose, up to 2 cm. in diameter, often forming small pincushion-like rosettes usually thickly covered with apothecia, yellow, orange-yellow or greenish-yellow, composed of many short, 1 mm. long, narrow, up to 0.5 mm. broad lobes. The lobes flat and appressed or tightly imbricated, almost erect in the thalli which are cushion-shaped. Underside pale with a few pale rhizoids. No soredia or isidia. Apothecia very abundant, up to 4 mm. broad, adnate or sessile, the disk concave to flat, dark orange, the exciple concolorous with the thallus, smooth to crenate. Hymenium and hypothecium hyaline. Spores two-celled, polar, hyaline, ellipsoid 11-18 x 5-8 μ. Thallus and apothecia KOH + purplish-red except in f. *chlorina*.

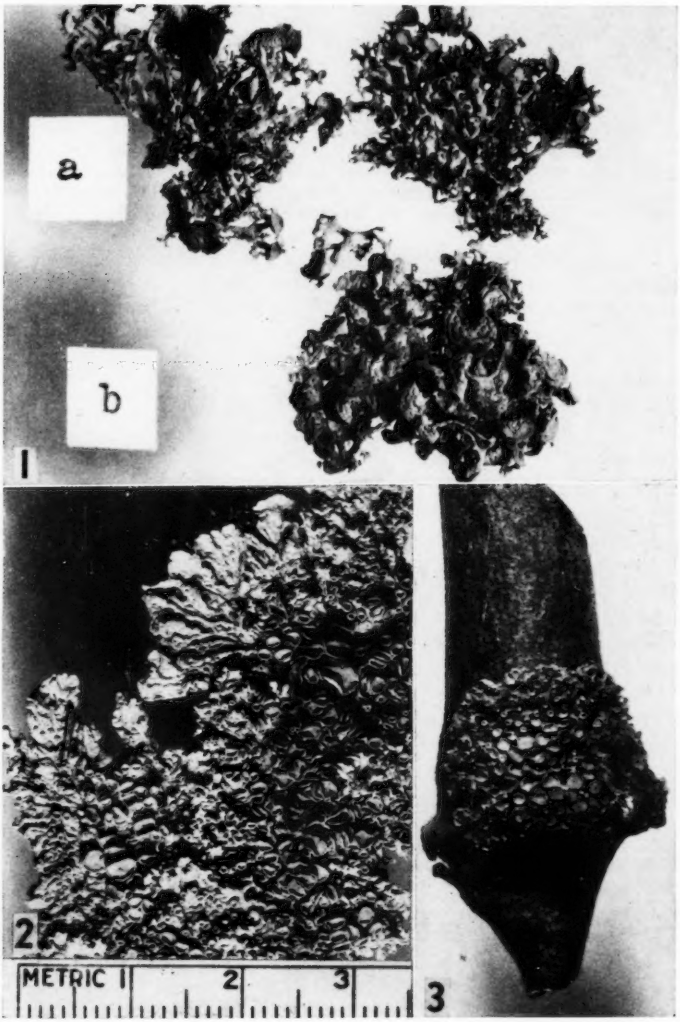
In northern Wisconsin this species is very common, especially on aspens, along with *Caloplaca cerina* and *Physcia stellaris*.

ADAMS CO.: Leola, 1935; ASHLAND CO.: Ashland, 1922, *R. H. Denniston;* BARRON CO.: Barron, 1930, *L. S. Cheney;* BAYFIELD CO.: Mason, 1896, *L. S. Cheney;* DANE CO.: Madison, 1916, *C. Audrey Richards;* Stevens Hill, Madison, 1893, *Heald and Buell;* DOUGLAS CO.: Brule River Valley, 1946; Foxboro, 1942, east of Superior, 1942; falls of Copper Creek, 1942; Pattison State Park, 1942; LINCOLN CO.: 9 miles northeast of Merrill, 1946; MARATHON CO.: Granite Heights, 1894, *L. S. Cheney;* OCONTO CO.: 3 miles west of Oconto Falls, 1946; ONEIDA CO.: Tomahawk Lake, 1941; POLK CO.: Lewis, 1924, *J. J. Davis;* PORTAGE CO.: Stevens Point, 1894, *L. S. Cheney;* SAUK CO.: Parfrey's Glen, 1924, *R. H. Denniston;* Devils Lake, 1922, *R. H. Denniston;* VILAS CO.: Lost River, south of Sayner, 1938; northeast of Tomahawk Lake, 1941; Trout Lake, 1948; WASHBURN CO.: Minong, 1920, *R. H. Denniston;* Spooner, 1946, *R. I. Evans.*

2a. *Xanthoria polycarpa* f. *chlorina* Bouly de Lesd. Rech. Lich. Dun. 1 Suppl. 77. 1914.

Xanthoria polycarpa f. *chlorinoides* Hillm. Ann. Mycol. 18: 14. 1920.

This form is similar to the species except that it is greenish to grayish-yellow and is negative in reaction with KOH. As Hillman points out, it is a



Figs. 1-3.—1. *Teloschistes chrysopthalmus.* (a). Two thalli from Decades of North American Lichens No. 97, Annisquam, Mass. (b). One thallus from Madison, Wis., 1893. coll. Heald and Buell. 2. *Xanthoria parietina.* Specimen from Decades of North American Lichens No. 6, Annisquam, Mass. 3. *Xanthoria polycarpa.* Specimen from Spooner, Wis., coll. R. I. Evans.

shade form. All of the Teloschistaceae show analogous forms.

MARATHON CO.: near Granite Heights, 1946.

3. *Xanthoria candelaria* (Ach.) Arn. Flora 62: 364. 1879.

Lichen candelarius L. Spec. Plant. 1141. 1753, pr. p. *Lichen candelarius* Ach. Lich. Suec. Prodr. 92. 1798. *Parmelia parietina* var. *lychnea* Schaer. Enum. Crit. 50. 1850. *Physcia lychnea* Nyl. Lich. Scand. 107. 1861. *Xanthoria lychnea* Almq. Ofersigt. K. Vetensk. Akad. Förhandl. 32. 1879. *Parmelia parietina* var. *stenophylla* Wallr. Fl. Crypt. Germ. 1: 514. 1831. *Physcia controversa* Mass. Sched. Crit. 42. 1855. *Xanthoria controversa* Rabh. Krypt.-Flora Sachsen 2: 282. 1870. *Xanthoria lutea* Hillm. Verh. Bot. Ver. Brandenb. 74: 129. 1932.

Thallus small, irregular in shape to rosette-shaped, greenish-yellow to yellow or orange-yellow, pale below with sparse pale rhizoids. Lobes flat and narrow, often sharply incised, erect, seldom appressed, the margins sorediate and the apices becoming isidioid. Apothecia uncommon, up to 2 mm. in diameter, yellow to orange, exciple entire to sorediate, hymenium and hypothecium hyaline, spores 8, hyaline, 2-celled, polar, 9-16 x 5-9 μ. Thallus and apothecia KOH + red-purple.

This species is often confused with *Candelaria concolor* but the latter has 16 to 32 spores in the ascus. If sterile, the two may still be distinguished by the KOH reaction, the *Candelaria* being negative. Both have narrow yellow foliose lobes, somewhat raised and often granulose-sorediate at the margin.

The concepts of *Toloschistes candelarius* in Fink's "Flora" and *T. lychneus* in Tuckerman's "Synopsis" include both this species and the following, *X. fallax*, which is a markedly distinct plant.

Usually the apices are long isidioid, but in collections of this species found in Wisconsin the isidia are very short-coralloid, characterstic of var. *finmarkica*, or the thallus is almost lost in masses of soredia, a characteristic of var. *leprosa*. No typical *X. candelaria* has yet been collected in Wisconsin.

3a. *X. candelaria* var. *finmarkica* (Ach.) Hillm.; Rabenh. Deuts. Krypt.-Fl. 9[6]: 26. 1935.

Lecanora candelaria var. *finmarkica* Ach. Syn. Lich. 192. 1814. *Borrera pygmaea* Bory apud Moug. et Nestl. Stirpes Crypt. Vogeso-rhenanae 8: 743d, 1843. *Xanthoria candelaria* var. *pygmaea* Hillm. Hedw. 63: 202. 1922. *Xanthoria candelaria* f. *finmarkica* A. Zahlbr. Cat. Lich. Univ. 7: 282. 1931.

Thallus of small, round rosettes, the lobes erect, very small, with the tips and sides of the lobes covered with short coralloid isidia.

DANE CO.: 20 miles west of Madison, 1938.

3b. *Xanthoria candelaria* var. *leprosa* (Lamy) Hillm. Hedw. 63: 202. 1922.

Physcia lychnea var. *leprosa* Lamy Cat. Lich. Mont-Dore 46. 1880.

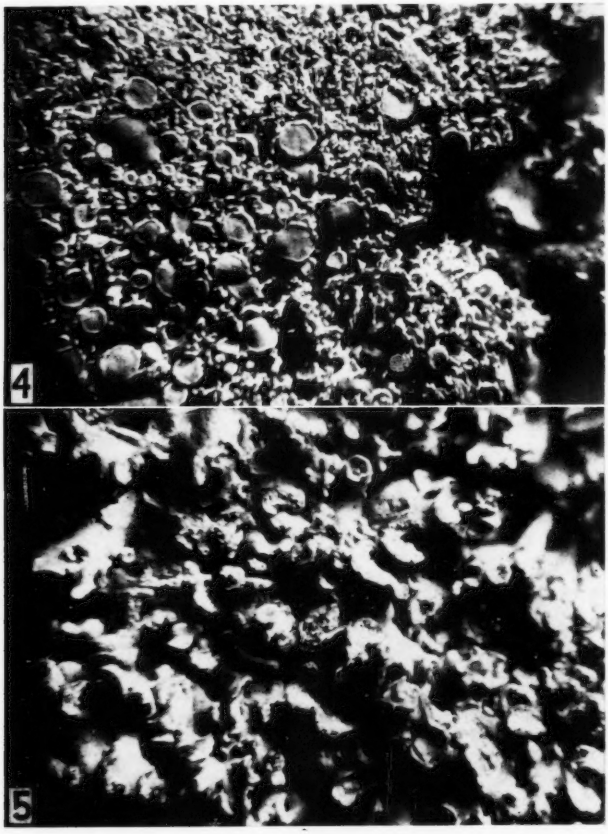
Thallus lobes covered with soredia, small, only showing here and there, KOH + purplish-red.

There is a very close similarity of appearance between this variety and *Candelaria concolor* var. *effusa*, but the KOH reaction will immediately serve to separate the two, the *Candelaria* being KOH–. Both may be found on trees or on rocks.

ROCK CO.: on limestone of a quarry T. 4 N., R. 12 E., Sec. 12, Newville, 1946.

4. *Xanthoria fallax* (Hepp) Arn. Verh. Zool. Bot. Ges. Wien 30: 121. 1880.

Physcia fallax Hepp apud Arn. Flora 41: 307. 1858. *Placodium fallax* Hepp. Flecht.



Figs. 4, 5.—4. *Xanthoria candelaria* ×6. From a specimen of Malme Lich. Suec. Exsic. No. 935 in the Herbarium of the University of Wisconsin. 5. *Xanthoria fallax* ×6. From No. 62 of Lich. Wis. Exs.

Eur. 11, No. 633. 1860. *Xanthoria lychnea* var. *fallax* Lahm Zusammenstell. Westf. Beob. Flecht. 53. 1885. *Lichen candelarius* var. *substellaris* Ach. apud Westr. Svenska Lafv. Färgh. 12, 21. 1805. *Lecanora candelaria* var. *substellaris* Ach. Lich. Univ. 417. 1810. *Xanthoria substellaris* Vain. Etude Lich. Bres. 1: 71. 1890. *Physcia ulophylla* Stizbg. Lich. Helvet. 69. 1882. *Xanthoria ulophylla* Arn. Lich. Fränk. Jura. 78. 1885. *Xanthoria lychnea* var. *ulophylla* Lett. Hedw. 52: 243. 1912. *Physcia parietina* var. *sorediosa* Nyl. Bull. Soc. Bot. Fr. 13: 366. 1866.

Thallus from small rosettes to covering large areas of the substrate, dark yellow to deep orange. Lobes more or less erect, short, rounded, with soredia along the margins and on the undersides of the tips of the lobes in soralia; underside pale to darker with sparse, light colored rhizinae. Apothecia uncommon, disk orange, exciple concolorous with the thallus, hymenium hyaline, hypothecium hyaline to yellowish. Spores 8, hyaline, polar, 2 celled, 11-16 x 4.5-8 μ. Thallus and apothecia KOH + deep purple.

In Fink's "Flora" and Tuckerman's "Synopsis" this species and *Xanthoria candelaria* are united under the name *Teloschistes candelarius*. As Hillman has pointed out, typical material of each is easily distinguished but there is occasionally some difficulty. The formation of the soredia in soralia in *X. fallax* versus along the entire margin in *X. candelaria* is the most important character for their separation. Although the term soralia is often used in lichen literature, definite descriptions of it are hard to find. A soralium is a definitely margined area in which the cortex breaks up to form a mass of soredia. Soralia are present in *Xanthoria, Ramalina, Alectoria* and *Usnea*.

This species is the most abundant of the Wisconsin Xanthorias. Elm seems to be a favorite habitat and the ubiquitous roadside plantings make it common over the state. The plants seem to be usually lacking apothecia so that reproduction must take place largely by the abundant soredia.

ADAMS CO.: Leola, 1935; BARRON CO.: no locality, 1921, *R. H. Denniston;* 10 miles east of Rice Lake, 1946, *Homer Stevens;* BROWN CO.: Mill Center, 1946; CHIPPEWA CO.: 5 miles north of Bloomer, 1946; CLARK CO.: Fernwold, Worden tsp., 5 miles southeast of Stanley, 1947, *Margaret S. Bergseng;* DANE CO.: Assembly Grounds, Madison, 1893, *Heald and Buell;* Madison, 1928, *R. H. Denniston;* Blue Mounds, 1932, *R. H.* Denniston; DODGE CO.: Horicon, 1946; DOUGLAS CO.: on aspen bark at mouth of Amnicon River, 1942; Falls of the Amnicon River, 1942; FOND DU LAC CO.: among moss over rocks, 2 miles south of Hamilton, 1936; GREEN CO.: New Glarus Woods Park, 1946; GREEN LAKE CO.: Green Lake, 1946; IOWA CO.: Avoca, 1946; JEFFERSON CO.: 3 miles east of Ixonia, 1945; MARATHON CO.: Granite Heights, 1946; MARQUETTE CO.: Endeavor, 1946 (Lich. Wis. Exs. No. 12); OCONTO CO.: Little River west of Oconto, 1946 (Lich. Wis. Exs. No. 62); RICHLAND CO.: 5½ miles east of Viola, 1946; Gotham, 1946; SAUK CO.: Devil's Lake, 1932, 1933, *R. H. Denniston;* 4 miles west of Prairie du Sac, 1947, *N. C. Fassett;* Sauk City, 1924, *R. H. Denniston;* southwest of Prairie du Sac, 1946; TREMPELEAU CO.: 1 mile east of Centerville, 1946; WAUKESHA CO.: 1 mile east of Golden Lake, 1945; Martin's Woods, Big Bend, 1945; WAUSHARA CO.: Wild Rose, 1946; WINNEBAGO CO.: Waukau, 1945; WOOD CO.: Wisconsin Rapids, 1946.

4a. *Xanthoria fallax* f. *chlorina* Anders Hedw. 63: 317. 1922.

Xanthoria substellaris f. *chlorina* Hillm. Rabenh. Krypt.-Fl. 96: 30. 1935.

This is merely a shade form of the species with greenish-yellow to grayish-yellow color.

CHIPPEWA CO.: on bark of Ostrya, 5 miles north of Bloomer, 1946.

5. *Teloschistes chrysopthalmus* (L.) Th. Fr. Gen. Heterolich. Europ. 51. 1861.

Lichen chrysopthalmus L. Mant. alt. 311. 1771. *Borrera chrysopthalmus* Ach. Lich. Univ. 502. 1810. *Physcia chrysopthalma* Schaer. Enum. Crit. 12. 1850. *Tornabenia chrysopthalma* Mass. Mem. Lichenogr. 42. 1853.

Thallus short fruticose, up to about 2 cm. long, in tufts, greenish-yellow or grayish-yellow to dark orange. Lobes flat, narrow, up to 1.5 mm. broad, branched more or less dichotomously, margins more or less ciliate, lacking soredia or isidia, sometimes more or less reticulately ridged. Apothecia common, 1-7 mm. broad, disk orange-yellow, exciple lighter and ciliate. Hymenium and hypothecium hyaline. Spores 8, hyaline, polar 2-celled, 10-17 x 6-8 μ. Thallus and apothecia purplish-red with KOH.

This is a handsome species, common in the southern United States, but becoming rare northwards. It has been collected only once in Wisconsin. Fink distributed specimens from Iowa and Calkins reported it from several localities in Illinois. Fink reported it from Minnesota, noting that it was infrequent. Macoun reports it from Ontario and from Lake Winnipegosis, Manitoba, where he also reported *X. parietina*.

DANE CO.: On trees, Eagle Heights, Madison, 1893, *Heald and Buell*.

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Notes on Wisconsin Parasitic Fungi. XI.

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The collections on which this series of notes is based were made, unless otherwise indicated, in the season of 1945.

In my *Notes VI* (Trans. Wis. Acad. Sci. 36. 1944) a gross typographical error occurs in the middle of page 261. It should read '*Helminthosporium rostratum* Drechsler on *Eragrostis cilianensis*' instead of '*Helminthosporium leucostylum* Drechsler on *Eleusine in- ilianensis*.'

Calopogon pulchellus fruits, collected by J. T. Curtis at Helmet Lake, Vilas Co., November 1935, bear prominently developed sclerotia. Since the material was obtained so late in the season it is not certain that the fungus was parasitic.

Asclepias sullivantii bore sterile, black, friable, carbonaceous growths on the living leaves. The growths are 2-5 mm. diam., and amphigenous in the sense that they extend entirely through the leaf. They are slightly elevated, somewhat flattened, and zonate in the case of the larger ones. They seem to be definitely fungal in nature and, if they were insect induced, it is not evident. Faville Prairie near Lake Mills, Jefferson Co., August 30.

"SPHAERIA SOLIDAGINIS" Schw., a sclerotial growth of dubious affinities, occurred on leaves of *Aster lucidulus* at Madison in September. Farlow, in his *Bibliographical Index*, stated that this fungus is, in many cases at least, a parasite of *Coleosporium solidaginis* and is probably a *Darluca*. The specimen on *A. lucidulus* appears as though it might be parasitic on *Coleosporium*, but there is no suggestion of *Darluca*.

PERONOSPORA PARASITICA on cultivated radish was used by E. M. Gilbert for instructional purposes over a period of many years. He informs me that he has always found the *Peronospora* on this host as an overgrowth of old lesions caused by *Albugo*. A more or less pronounced blackening accompanies this secondary development.

Powdery mildews which failed to form perithecia parasitized the following hosts, not previously reported as infected by them in Wisconsin: *Potentilla arguta*, Dane Co., Pine Bluff, June 29; *Asclepias amplexicaulis*, Dane Co., Madison, August 20; *Solanum carolinense*, Madison, August 25; *Rudbeckia hirta*, Madison, August 26; *Grindelia squarrosa*, Iowa Co., Blue Mounds, September 11, 1934.

CORDYCEPS CAPITATA Fr. was found in late September in white pine woods at Parfrey's Glen, Sauk Co. This is assumed to have been parasitic on some species of *Elaphomyces*, but unfortunately at the time of collection the nature

of the fungus was not realized and it was taken without the subterranean host. E. M. Gilbert states that he collected this on *Elaphomyces* in Wisconsin some thirty years ago.

Betula papyrifera leaves, collected August 17 at Madison, bear large, irregular, brown spots with bright yellow margins. A melanconiaceous fungus is epiphyllous on the spots. It appears to be probably the same thing which Davis reported as *Sacidium microspermum* (Pk.) Davis (*Septoria microsperma* Peck), later renamed *Cylindrosporella microsperma* by Petrak (Ann. Mycol. 22: 43. 1924). It is questionable whether *Cylindrosporella* is distinct from *Gloeosporium*. *Sacidium* is also a dubious genus. Kabat and Bubak in 1907 described *Gloeosporium leptothyrioides* which, it now appears to me, is in all probability Peck's fungus. If the species is finally to be placed under *Gloeosporium* Peck's specific epithet should be used, provided it is not preempted. It is possible that this might be considered a *Leptothyrium*, but it is evidently not *L. betulae* Fckl. which has much smaller conidia. Provisionally, I am filing my specimens under *G. leptothyrioides* Kab. & Bub.

PHYLLOSTICTA sp. occurred in profusion at Madison on living leaves of *Ratibida* (*Lepachys*) *pinnata*. This is perhaps the precursor of a perfect stage and is possibly connected with *Septoria lepachydis* Ell. & Ev. The pycnidia are gregarious on conspicuous, round to orbicular, arid spots which are mostly 2-3 mm. diam. The pycnidia are 115-160 μ diam., subglobose, rostrate, sooty brown, of loosely pseudoparenchymatous texture, and apparently amphigenous, although more erumpent and thus more readily observable on the upper leaf surface. The hyaline, bacilliform conidia are about 4-6 x 1.5-2 μ.

PHYLLOSTICTA sp. on *Zizia aptera* (*cordata*). Madison, October 3. The large black pycnidia are on rounded, ash-brown spots, the ellipsoid conidia about 7 x 3 μ. There seems to be no record of any *Phyllosticta* on *Zizia*, but this specimen is inadequate for descriptive purposes.

PHYLLOSTICTA sp. on *Helianthus occidentalis*. Dane Co., near Sauk City, September 5. On large fusoid to orbicular, brownish-purple lesions. The hyaline conidia are about 8-11 x 3 μ, the few pycnidia measured, about 125 μ diam. This host is very liable to spotting and it is rather doubtful that the lesions were caused by the fungus. A very similar, if not identical, fungus has been noted on *Helianthus rigidus* from the same station.

ASCOCHYTA sp. on mint geranium, *Chrysanthemum balsamita* var. *tanacetoides*, has been collected in several different years at a station near Madison. The host is firmly established in a long-abandoned farm garden. Because of seeming microscopic similarity of this fungus to a European species, occurring on a closely related host, which I have been unable to examine, I have refrained from describing it. However, excellent material has been obtained and it seems worth while to offer the following descriptive notes: Spots rounded, ashen with rather wide, dark brown borders, 2-7 mm. diam., one to several per leaf; pycnidia mostly epiphyllous, scattered, one to a dozen or more per spot,

sooty-brown, narrowly ostiolate, subglobose, about 125-175 μ diam.; conidia cylindric, hyaline, frequently biguttulate, 8-12 x 2.5-3 μ.

SEPTORIA ARTEMISIICOLA on *Artemisia serrata* (from Tomah, Wis.) was described by Davis (Trans. Wis. Acad. Sci. 30: 14. 1937). Whether this can with certainty be differentiated from *Cylindrosporium artemisiae* Dearn. & Barth. seems questionable. In a recent collection on the same host from Mazomanie, Dane Co., which I am tentatively placing under *S. artemisiicola,* the epiphyllous pycnidia (or acervuli ?) are very deeply sunken, so as to occupy the entire leaf space, from upper to lower epidermis. They are imperfect at the top and scarcely seem good pycnidia. On the lower side of the leaf are numerous immature perithecia, containing asci with undifferentiated contents. Unlike the pycnidia, these are almost superficial. They do not appear to be *Acanthostigma,* so frequently encountered on *Artemisia.*

RAMULARIA RUFOMACULANS Peck on *Polygonum natans* f. *hartwrightii,* in an abnormal late season development, perhaps due to cold weather, is characterized by the production of vast numbers of extremely short, 5-6 μ, ellipsoid conidia, with only occasional longer ones, and is on bluish-gray spots with a water-soaked appearance, noticeable only on the under surface of the leaf.

The geographical position of Wisconsin in the prairie-forest transition zone provides conditions which lead to problems of ecological interest concerning the present-day distribution not only of phanerogams, but of the fungi, particularly rusts and smuts, which parasitize them. There seems to be good evidence that present climatic conditions are of recent origin and that it is not more than twelve hundred years since the close of a xerothermic period which favored prairie over the forest. It is the consensus of opinion that the present climate favors forest over prairie and that, if no further climatic shift occurs, that portion of our flora characteristic of the prairie will disappear. At present, however, prairie species are still well represented. It is of considerable interest to me that some of the parasites which are evidently of common occurrence on certain prairie hosts farther west have not yet been found on the same hosts in Wisconsin, despite intensive collecting in this state over a sixty year period. It cannot of course be demonstrated that these parasites ever occurred in Wisconsin, but one is led to wonder whether their current absence may not be due to an even greater sensitivity than their hosts to changed environmental conditions. Perhaps also the hosts themselves have undergone subtle changes which alter or minimize the chances of infection by certain parasites.

ADDITIONAL HOSTS

The following hosts have not been previously recorded as bearing the fungi mentioned in Wisconsin.

BASIDIOPHORA ENTOSPORA Roze & Cornu on *Aster oblongifolius* var. *angustatus.* Columbia Co., Black Hawk's Lookout near Prairie du Sac, August 15. Although the xerophytic host is highly localized, it sometimes occurs in massive profusion on the steep bluffs overlooking the Wisconsin River Valley,

thus perhaps facilitating infection by a downy mildew of a host that one would not consider a favorable substrate when growing in its usual scattered habit.

ERYSIPHE GRAMINIS DC. Perithecia on *Agropyron subsecundum*. Sauk Co., Devils Lake, August 24. The asci have been delimited, but as usual there is no evidence of ascospore formation.

ERYSIPHE POLYGONI DC. on *Anemonella thalictroides*. Dane Co., near Sauk City, August 10. Coll. M. S. Bergseng; conidia only on *Trifolium hybridum*. Dane Co., Madison, August 25.

ERYSIPHE CICHORACEARUM DC. on *Mentha arvensis* var. *canadensis*. Dane Co., Madison, September 3. This is in good maturity and seems unmistakable on morphological grounds. There is, however, considerable uncertainty concerning the powdery mildews on this and other hosts in the Labiatae. In an earlier record I mentioned the occurrence of presumed *Erysiphe galeopsidis* on this host and on *Stachys palustris*.

ERYSIPHE GALEOPSIDIS DC. on *Eupatorium urticaefolium* (*E. ageratoides*). Dane Co., Madison, August 20. Salmon in his monograph of the powdery mildews (Mem. Torrey Club 9: 208. 1900) in writing of the similarity of *Erysiphe cichoracearum* and *E. galeopsidis* states "Among some American examples, however, I was surprised to find in two specimens named *E. cichoracearum* on *Eupatorium ageratoides* (one from Madison, Wisconsin, Sept. 1882, L. H. Pammel) in Professor Earle's herbarium . . . haustoria of exactly the same size and shape as those on examples of *E. galeopsidis* on *Galeopsis*. Unfortunately both these specimens are rather young, and the asci contain no spores. It is, therefore, impossible to say whether we have in this case a form of *E. cichoracearum* with lobed haustoria, or whether it may not possibly be that *E. galeopsidis*, hitherto supposed to be confined to Labiatae and *Chelone* among Scrophularineae sometimes occurs on Compositae. In another case the fungus is undoubtedly *E. cichoraceaurm*." In the 1945 specimen the large perithecia are imbedded in a profuse superficial mycelium, the asci where formed lack ascospores, and thin free-hand sections stained with cotton blue showed lobed haustoria. As Salmon suggests, the relationship between *E. cichoracearum* and *E. galeopsidis* seems very close indeed.

MICROSPHAERA DIFFUSA C. & P. on *Desmodium illinoense*. Dane Co., Madison, September 21. There do not seem to be earlier reports of any powdery mildew on this host.

MICROSPHAERA ALNI (Wallr.) Wint. on *Syringa persica* (cult.). Dane Co., Madison, October 14.

PHYLLACHORA GRAMINIS (Pers.) Fckl. on *Agropyron subsecundum*. Columbia Co., Black Hawk's Lookout near Prairie du Sac, August 15.

ROSENSCHELDIA HELIOPSIDIS (Schw.) Theiss. & Syd. on *Helianthus rigidus*. Dane Co., Madison, September 12. The characteristic large *Phyllosticta*-type conidia are present, but asci have not been developed.

COLEOSPORIUM VIBURNI Arth. II, III on *Viburnum opulus* (cult.). Dane Co., Madison, September 16. Arthur's Manual does not list this host, nor is it mentioned in Oudemans as bearing any rust. The plants were in a nursery in close proximity to very heavily infected specimens of *Viburnum lentago*. *V. trilobum*, the native high bush cranberry, usually grows isolated in low thickets, so that probably there is not much chance for infection. At any rate, the rust has not yet been reported on it from Wisconsin or elsewhere.

PUCCINIA CORONATA Cda. III on *Agrostis gigantea* var. *dispar* (*A. alba* of Gray's Manual, 7th ed.). Dane Co., Madison, September 8. *Arthur's Manual* gives Oregon as the only locality for the rust on this host.

PUCCINIA HELIANTHI Schw. II, III on *Helianthus occidentalis*. Dane Co., Madison, August 17. According to *Arthur's Manual*, known on this otherwise only from Iowa.

ACANTHOSTIGMA OCCIDENTALE (Ell. & Ev.) Sacc. on *Antennaria parlinii*. Sauk Co., Parfrey's Glen, Town of Merrimac, September 26. In view of the diverse conidia that are encountered from pycnidia having the morphology of this species, it is quite probable that more than one species is involved. In the present case the conidia are rod-shaped, 6-10 x 1.5-2 μ. Perithecia were not observed.

SEPTORIA PHYSOSTEGIAE Ell. & Ev. on *Physostegia parviflora*. Jefferson Co., Faville Prairie near Lake Mills, August 30. Host det. by N. C. Fassett. Davis lists only *Physostegia virginiana* as a host, but Fassett considers that that species, as currently understood, probably does not occur in Wisconsin.

COLLETOTRICHUM FUSARIOIDES (Ell. & Kell.) O'Gara on *Asclepias sullivantii*. Jefferson Co., Faville Prairie near Lake Mills, August 30. Seemingly the first report of a parasite on this host.

ELLISIELLA CAUDATA (Pk.) Sacc. on *Sporobolus heterolepis*. Dane Co., Madison, September 21. It is not certain that this developed parasitically, but it seems likely. The affected leaves are dead throughout.

TITAEOSPORA DETOSPORA (Sacc.) Bubak on *Equisetum laevigatum*. Dane Co., Madison, September 8.

RAMULARIA TULASNEI Sacc. on *Fragaria vesca* var. *americana*. Dane Co., Madison, August 26. Trelease may have collected the fungus on this host, but his account is not clear, and Davis put no specimens in the herbarium.

CERCOSPORELLA DEARNESSII Bub. & Sacc. on *Solidago riddellii*. Dane Co., Madison, August 25. In this collection the conidiophores are mostly from 50-65 μ long. In the description the narrow range of 65-75 μ is given. For *Cercosporella nivea* Ell. & Barth. the conidiophore length is specified as 15-25 μ. It may be doubted that these species are really distinct, since intergrading forms occur, but in the absence of certain knowledge it seems best to keep them separate for the present.

CLADOSPORIUM ASTERICOLA J. J. Davis on *Aster oblongifolius* var. *angustatus*. Columbia Co., Black Hawk's Lookout near Prairie du Sac, August 15.

POLYTHRINCIUM TRIFOLII Kze. on *Trifolium hybridum*. Sauk Co., Devils Lake, August 24. Although this has undoubtedly often been observed in Wisconsin before, it seems not to have been mentioned in Davis' or my notes, so is included for the sake of a complete record.

HELMINTHOSPORIUM ROSTRATUM Drechsler on *Eragrostis spectabilis*. Dane Co., Madison, September 8. Seymour does not list *H. rostratum* on this host which is, incidentally, *E. pectinacea* of *Gray's Manual*, 7th ed. I have consistently followed the treatment of Deam in his *Flora of Indiana* in determinations of *Eragrostis*, so that an earlier report by me of *H. rostratum* on *E. pectinacea* does not refer to *E. spectabilis*.

CERCOSPORA RHOINA Cke. & Ell. on *Rhus typhina*. Dane Co., Madison, August 25.

CERCOSPORA VERBASCICOLA Ell. & Ev. on *Verbascum thapsiforme*. Dane Co., Madison, October 4. I find no previous report of *Cercospora* on this host.

CERCOSPORA TRIFIDAE Chupp on *Ambrosia artemisiifolia*. Dane Co., Madison, August 26, 1944. This has been previously recorded (on *A. trifida*) in Wisconsin as *Cercospora ferruginea* var. *ambrosiae* (Seym. & Earle) J. J. Davis.

ADDITIONAL SPECIES

The fungi mentioned have not been previously reported as occurring in Wisconsin. Type specimens of new species and varieties have been placed in the University of Wisconsin Cryptogamic Herbarium.

STAMNARIA AMERICANA Mass. & Morg. on *Equisetum hyemale*. Sauk Co., Parfrey's Glen, Town of Merrimac, September 26. This is a vigorous parasite and was present in great profusion. There seems to be considerable variation in size of asci and ascospores, but the larger are far out of the range of those of *Stamnaria equiseti* (Hoffm.) Rehm. There seems little doubt that the species of *Titaeospora*, presumably *T. detospora* (Sacc.) Bub., which is found on Equisetum in Wisconsin is the imperfect stage of *Stamnaria*.

ENTYLOMA IRREGULARE Johans. on *Poa pratensis*. Dane Co., Madison, September 18. The dark sorus superficially resembles a long covered telium. The spores in mass have a smoky hue, but viewed individually are not dark.

USTILAGO SPEGAZZINII Hirsch. and U. SPEGAZZINII var. AGRESTIS Fisch. & Hirsch. on *Stipa spartea*. Fischer and Hirschorn (Mycologia 37: 236. 1945) treat at length of the smut which occurs in Wisconsin on *Stipa*, and which has been reported as *Ustilago hypodytes* (Schl.) Fr. They find that this name has been applied to a complex of smut fungi rather than to a single species. They set aside *U. spegazzinii* Hirsch., originally described from the

Argentine, as a species whose spores have bipolar areas or appendages, and cite a collection of J. J. Davis from Meridean, Dunn Co., Wis. as being representative. Even under oil immersion I find it difficult to discern the "minutely echinulate epispore typical of *U. Spegazzinii,*" but the bipolar crests are prominent. A Davis specimen from Blue River, Grant Co., seems to be the same thing, but two specimens from Arena, Iowa Co., collected in 1929 and 1935, lack the crests. So far as the specimens show, the smut is confined to the inflorescence and I take it they should be assigned to *U. spegazzinii* var. *agrestis* Fisch. & Hirsch.

PUCCINIA SPOROBOLI Arth. II, III on *Sporobolus heterolepis.* Dane Co., near Sauk City, September 5. An eastward extension of the Manual range, which is given as "locally on prairies from southern North Dakota, southward to central Iowa and Nebraska"

PUCCINIA ACETOSAE (Schum.) Körn. II on *Rumex acetosella.* Sauk Co., sand barrens, 2 miles west of Spring Green, September 17.

Phyllosticta zanthoxyli sp. nov.

Maculis orbicularibus, brunneis, marginibus fuscis angustissimis, 4-8 mm. diam.; pycnidiis gregariis, fuscis, subglobosis, ostiolatis, 150-180 μ diam. ca.; conidiis hyalinis, granulosis, ellipsoideis vel subfusoideis, magnis, 16-26 x 6-8 μ.

Spots orbicular, brown, with a very narrow dark brown margin, 4-8 mm. diam.; pycnidia gregarious, blackish brown, subglobose, ostiolate ,about 150-180 μ diam.; conidia hyaline, granular, ellipsoid or subfusoid, large, 16-26 x 6-8 μ.

On living leaves of *Zanthoxylum americanum.* Madison, Dane Co., Wisconsin, U. S. A., September 8, 1945.

There is no evidence of septation in the elongate conidia and hundreds were observed in a number of mounts. There is indication of insect action in connection with some of the lesions, so the parasitism of the fungus may be open to question, since it cannot be determined whether fungus preceded insect, or vice versa. *Macrophoma zanthoxyli* Ell. & Ev., described as on dead branches of *Zanthoxylum* sp. from Louisiana has spores of the same size as those of *P. zanthoxyli,* but the pycnidia are said to be quite small, while those of the species here described are of more than average size.

PHYLLOSTICTA TILIAE Sacc. & Speg. on *Tilia americana.* Dane Co., Madison, August 20. The spots on this host are much smaller and more definite than those in specimens on the European host, *Tilia platyphylla,* but the fungus is identical microscopically. In the description the spots are stated to be diverse.

Ascochyta hydrophylli-virginiani sp. nov.

Maculis nigris obscuris, rotundatis vel irregularibus, saepe apicibus paginis coopertis, magnis, interdum 1.5 cm. diam., indistincte zonatis; pycnidiis incon-

spicuis, epiphyllis, gregariis, pallido-olivaceis, subglobosis, ostiolatis, muris tenuibus, 90-130 μ diam.; conidiis hyalinis, cylindraceis, 1-septatis, 10-15 x 3.5-4 μ.

Spots dull black, rounded or irregular, often involving tips of leaflets, large, sometimes 1.5 cm. diam., faintly zonate; pycnidia inconspicuous, epiphyllous, gregarious, pale olivaceous, subglobose, ostiolate, thin-walled, 90-130 μ diam.; conidia hyaline, cylindrical, 1-septate, 10-15 x 3.5-4 μ.

On living leaves of *Hydrophyllum virginianum*. Madison, Dane County, Wisconsin, U. S. A., October 4, 1945.

A similar fungus collected at Madison in June 1944 (Amer. Midl. Nat. 34: 261. 1945) probably belongs with this species. Spore maturity seems to run by pycnidia, that is, all the conidia in any one pycnidium are mature and septate, or all, except perhaps a very few, lack septation. The conidia are much wider than those of *Ascochyta hydrophylli* Sprague & Bailey.

Stagonospora tephrosiae sp. nov.

Maculis variis, plerumque immarginatis, angulatis vel irregularibus, pallido-brunneis, vel marginatis, parvis, rotundatis, centris pallido-brunneis, fuscis cingulatis; pycnidiis erumpentibus sed basibus immersis, fuscis, epiphyllis, conspersis, variis, subglobosis vel obovatis, indistincte ostiolatis, 70-120 x 100-160 μ; conidiis hyalinis, ellipsoideis, curto-cylindraceis vel cylindraceis vel subclavatis, rectis vel curvis, 1-6-septatis, 10-35 x 6-11 μ.

Spots variable, mostly immarginate, angled or irregular, pale brown, or marginate and small, rounded, centers pale brown, borders dark; pycnidia erumpent but their bases deeply sunken in the substratum, dark brown, epiphyllous, scattered, variable, subglobose or obovate, indistinctly ostiolate, approx. 70-120 x 100-160 μ; conidia hyaline, ellipsoid, short-cylindrical or cylindrical or subclavate, straight or curved, 1-6-septate, 10-35 x 6-11 μ.

On living leaves of *Tephrosia virginiana*. Madison, Dane County, Wisconsin, U. S. A., August 16, 1945.

This interesting species was mentioned in an earliier note (Trans. Wis. Acad. Sci. 35: 121. 1943). The pycnidia are unusual in the frequently obovate shape. That is to say, the deeply imbedded basal portion is markedly narrower than the part projecting above the leaf surface. As indicated, the conidia are highly variable, ranging from 10-35 x 6-11 μ with considerable differences in shape, and this variation may occur within a single pycnidium. In spite of this the conidia all appear well-matured and exhibit a definite constancy of aspect. In a good many of the conidia which show curvature the cross walls are not parallel to one another, and occasionally there are slight constrictions at the septa. Seemingly, there are no morphologically distinguishable conidiophores.

Stagonospora macromaculans sp. nov.

Maculis conspicuis, orbicularibus, centris cinereis, marginibus fuscis latis variis, plerumque magnis, 5-20 mm. diam.; pycnidiis gregariis, amphigenis, erumpentibus, subcuticularibus, nigris, subglobosis, subrostratis, ostiolatis, 150-

300 μ diam.; conidiis hyalinis, granulosis, flexuosis vel curvis, tenuatim, 6-11-septatis, 75-115 x 8-11 μ.

Spots conspicuous, orbicular, cinereous in center, fuscous margin of varying width, mostly large, 5-20 mm. diam.; pycnidia gregarious, amphigenous, erumpent, subcuticular, black, subglobose, subrostrate, ostiolate, 150-300 μ diam.; conidia hyaline, granular, flexuous or curved, tapered, 6-11-septate, 75-115 x 8-11 μ.

On living leaves of *Celtis occidentalis*. Madison, Dane County, Wisconsin, U. S. A., September 2, 1945.

Some of the pycnidia are more markedly rostrate than others. The ostiole is very sharply defined, being composed of a tightly packed ring of dark, narrow, brick-like cells which contrast strongly with the ordinary pseudoparenchymatous cells which impinge on them.

HENDERSONIA CELTIFOLIA Cooke on *Celtis occidentalis*. Dane Co., Madison, August 4, 1944. Cooke described this species as with spores fuscous, triseptate, 15-25 x 8 μ. In my specimen they are dark and uniformly triseptate, but most of the spores are from 15-20 x 5-7 μ. Doubtfully parasitic. The fruiting bodies are on areas which may have become moribund following insect attack, so common on this host.

Septoria scrophulariae Peck var. **agalinis** var. nov.

Pycnidiis parvis, 60-70 μ diam.; conidiis flexuosis, sed non fortiter curvis, 17-40 x 1.5-2 μ.

On living leaves of *Gerardia* (*Agalinis*) *paupercula*. Madison, Dane County, Wisconsin, U. S. A., September 3, 1945.

In general aspect, type of spot, and color and arrangement of pycnidia on the spot, this is at once suggestive of *Septoria scrophulariae*. The fungus on *Gerardia* differs in having pycnidia only two-thirds, or less, the size of those on *Scrophularia*, and in generally shorter, more slender, and flexuous, rather than strongly curved sporules. As a host substratum, *Gerardia paupercula*, with its slender, highly cutinized leaves, is far from lush, and this may be a factor in the smaller size of the fungus.

Phaeoseptoria festucae var. **andropogonis** R. Sprague var. nov.

Maculis ochraceis, marginibus purpureis, ellipsoideis, pycnidiis paucis, nigris, subglobosis, tarde ostiolatis, 190-205 μ diam. ca.; pycnosporulis 60-85 x 5.5-7.5 μ, flavidis, clavato-filiformibus vel obclavatis, basis subacutis vel subobtusis, apicibus acutis, 5-11-septatis.

Spots ochraceous, with purple margins, ellipsoid; pycnidia few, black, subglobose, tardily ostiolate, approx. 190-205 μ diam.; pycnospores 60-85 x 5.5-7.5 μ, yellowish, clavate-filiform or obclavate, base subacute or subobtuse, apex acute, 5-11-septate.

On living leaves of *Andropogon furcatus* (associated with *Stagonospora*

sp.). Sauk County, sand barrens, one mile northeast of Spring Green, Wisconsin, U. S. A., August 22, 1945. Coll. H. C. Greene.

As Sprague points out, this variety has spores considerably larger than either *Phaeoseptoria festucae* or *P. festucae* var. *muhlenbergiae*. Besides the type locality, I have also found this on the same host in Dane Co., near Sauk City. As in the type collection, the *Phaeoseptoria* is closely associated with *Stagonospora*.

Ramularia chimaphilae sp. nov.

Maculis conspicuis, rotundatis, 3-10 mm. diam., centris cinereis, marginibus latis, fuscis; conidiophoris fasciatis, fasciis compactis, gregariis vel confertis, amphigenis, saepe 100 μ diam.; conidiophoris hyalinis, variis, plerumque fere obsoletis, interdum 12 μ vel magis leviter, exilibus, 2.5-3 μ latis; conidiis hyalinis, rectis, exilibus, truncatis, fortiter catenulatis, continuis vel 1-septatis, 10-35 x 2.5-3 μ.

Spots conspicuous, rounded, 3-10 mm. diam., center cinereous, margin wide, fuscous; conidiophores in tufts, tufts compact, gregarious or crowded, amphigenous, often as much as 100 μ diam.; conidiophores hyaline, variable, mostly almost obsolete, sometimes up to 12 μ or slightly more, slender 2.5-3 μ wide; conidia hyaline, straight, slender, truncate, markedly catenulate, continuous or 1-septate, 10-35 x 2.5-3 μ.

On living leaves of *Chimaphila umbellata*. Parfrey's Glen, Town of Merrimac, Sauk County, Wisconsin, U. S. A., September 26, 1945.

The spots are most conspicuous and of similar appearance on both sides of the leaf. This is perhaps connected with the *Mycosphaerella* which is said to occur on *Chimaphila*, but which has not been collected in Wisconsin. The dark, tuberculate masses underlying the tufts of conidiophores are suggestive of this. *R. chimaphilae* is not a particularly characteristic species of *Ramularia*, but on an overall basis seems better assigned here than elsewhere. The compact tufts of conidiophores might possibly be regarded as sporodochia. The shorter conidia with their square ends recall *Oidium*, and the individual conidiophores, where discernible, are sometimes branched in a way that is reminiscent of illustrations of certain species of *Septocylindrium*. It is difficult to be certain that what seems to be a septum is not merely the point of attachment of a neighboring conidium, but in a number of cases it appears to be a real cross wall.

Cladosporium americanum sp. nov.

Hypophyllis, inconspicuis, nervisquentibus et in paginis; conidiophoris nonfasciculatis, sparsis, brunneis vel fuscis, infra rectis, frequenter fortiter et arte multisque supra geniculatis, non tortuis insignite, 2-4-septatis, 55-80 x 4.5-6 μ; conidiis pallido-olivaceis vel olivaceis, ellipsoideis vel curto-cylindraceis, obscure asperulis, cicatricibus prominentibus, continuis vel 1-septatis, 13-17 x 4-6 μ.

Hypophyllous, inconspicuous, nervisequous and on leaf blade; conidiophores non-fasciculate, scattered, brown to deep brown, straight below, fre-

quently strongly, closely and many times geniculate above, but not markedly tortuous, 2-4-septate, 55-80 x 4.5-6 μ; conidia pale olivaceous to olivaceous, ellipsoidal or short-cylindrical, faintly asperulate, scars prominent, continuous or 1-septate, 13-17 x 4-6 μ.

On living leaves of *Prunus americana*. Madison, Dane County, Wisconsin, U. S. A., September 18, 1944.

Most inconspicuous and detectable only with a lens. Best developed toward the leaf base and on the midrib. Younger conidiophores, from specimens collected in August 1945, are less strongly geniculate, but in other particulars the material corresponds to the 1944 collection. Frequently as many as 80% or more of the conidia in a mount are non-septate, a condition which is not at all unusual in this genus.

HELMINTHOSPORIUM DICTYOIDES Drechsler on *Festuca elatior*. Dane Co., Madison, September 18. Coll. & det. J. L. Allison.

Cercospora lithospermi Chupp & Greene sp. nov.

Maculis irregularibus, 1-3 mm. diam., vel saepe paginis amplis coopertis, initio pallido-olivaceis vel olivaceis, tarde rufo-brunneis vel prope nigris; fructificationibus hypophyllis plerumque; tuberculis intra stomatibus; fasciis densis, divergentibus; coniiophoris pallidis vel mediis olivaceo-brunneis, apicibus angustatis et prope hyalinis, 1-5-septatis, non geniculatis, non ramosis, rectis vel curvis vel undulatis, apicibus conicis, 3.5-6 x 15-50 μ; conidiis hyalinis, aciculatibus vel obclavatis, indistincte multiseptatis, rectis vel curvis, basibus truncatis, apicibus subacutis, 2-4 x 25-100 μ.

Spots irregular, when well-defined 1-3 mm. diam., or often involving much of the leaf, at first pale olivaceous or olivaceous, later reddish-brown or almost black; fruiting chiefly hypophyllous; stromata filling the stomatal openings; fascicles dense, divergent; conidiophores pale to medium olivaceous brown, much attenuated and nearly hyaline toward tip, 1-5-septate, not geniculate, not branched, straight to curved, or undulate, tip conic, 3.5-6 x 15-50 μ; conidia hyaline, acicular to obclavate, indistinctly multiseptate, straight or curved, base truncate, tip subacute, 2-4 x 25-100 μ.

On living leaves of *Lithospermum croceum* (*L. Gmelini* of *Gray's Manual*, 7th ed.; *L. carolinense* of Britton & Brown, Illus. Flora, ed. 2). Madison, Dane County, Wisconsin, U. S. A., September 26, 1945. Coll. H. C. Greene.

CERCOSPORA STACHYDIS Ell. & Ev. on *Stachys palustris*. Iowa Co., Arena, August 22. In the description of the type, the authors state that the conidia were immature. In my specimen the few conidia which are mature, and also those which are immature, show an extreme curvature. Mature conidia are about 100 μ long, hyaline, truncate at base, strongly tapered, 7-8-septate. The spots are 2-3 mm. diam., and are thus slightly larger than indicated in the description. Chupp has examined several collections of this fungus and he states that he has not observed the strong curvature of conidia that I find in

the Wisconsin specimens, but he thinks that if sufficient numbers of conidia were examined all gradations would be found.

Cercospora trifidae Chupp nom. nov.

Chupp considers that the ferruginous *Cercospora* which commonly occurs on *Ambrosia trifida* (occasionally also on *A. psilostachya* and *A. artemisiifolia*) and which has been variously designated as *Cercospora racemosa* var. *ambrosiae* Seym. & Earle and *Cercospora ferruginea* var. *ambrosiae* (Seym. & Earle) J. J. Davis is a variety of neither, but is an independent species, for which he proposes the new name *Cercospora trifidae*. He provides the following key to the three species of *Cercospora* which have been reported on *Ambrosia:*

A. Conidia hyaline, acicular, 1.5-4 x 25-195 μ; leaf spots brown, often with gray center ..... *C. arcti-ambrosiae.*

AA. Conidia colored, cylindric or only slightly attenuated, mostly wider than 4 μ.
B. Leaf spots distinct; fruiting not effuse, fascicles dense; conidia 6-10 x 20-95 μ ..... *C. ambrosiae.*

BB. Leaf spots indistinct, fruiting effuse, mostly non-fasciculate; conidia 3-5.5 x 15-65 μ ..... *C. trifidae.*

Notes on Wisconsin Parasitic Fungi. XII.

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The fungi referred to in this series of notes were, unless it is stated otherwise, collected during the season of 1946.

Powdery mildews which fail to produce perithecia, each season attack various host plants. Specific identification is uncertain, but there is no question as to parasitism. On some of the hosts the organisms occur regularly in the non-fruiting stage from year to year. It seems worth while to record these where there is no previous Wisconsin record of any powdery mildew on the host concerned. Examples observed in 1946 are *Pilea pumila,* Dane Co., Madison, September 27; *Erucastrum gallicum,* Madison, September 17; *Desmodium nudiflorum,* Sauk Co., Devils Lake, June 26; *Rhus copallina,* Columbia Co., Lodi, August 6; *Monarda punctata,* Dane Co., Pine Bluff, August 29; *Solidago sciaphila,* Sauk Co., Cactus Bluff, Town of Prairie du Sac, August 23; *Solidago speciosa,* Madison, September 15; *Solidago ulmifolia,* Sauk Co., Devils Lake, August 5; *Solidago patula,* Waukesha Co., Hartland, September 15; *Euthamia graminifolia,* Madison, September 15; *Aster ericoides,* Madison, July 5; *Helianthus rigidus,* Dane Co., Westport, September 10; *Rudbeckia laciniata,* Sauk Co., Parfrey's Glen, July 6 (widespread infection every year on this host); *Cacalia tuberosa,* Madison, July 22; *Lactuca ludoviciana,* Madison, August 27.

APIOSPORINA COLLINSII (Schw.) Hoehn. was found in mature condition on overwintered leaves of *Amelanchier canadensis* near Verona, Dane Co., in April. This fungus, which develops strongly on the host leaves during the summer and fall, evidently, on occasion at least, prevents the formation of an abscission layer, for the affected leaves remain conspicuously on the trees throughout the winter, persisting even after the new year's foliage starts to develop. This latter no doubt greatly facilitates infection of the tender new leaves by the mature ascospores. Previous Wisconsin collections of *A. collinsii* have all been immature.

PHYLLACHORA on *Sporobolus cryptandrus* was referred in an earlier publication to *Phyllachora graminis* (Pers.) Fckl. Orton, however, considers this to be *Ph. vulgata* Theiss. & Syd. So far as one can judge from Orton's treatment, the only way in which *Ph. vulgata* differs from *Ph. graminis* is in the generally lesser length of the ascomata, but even there overlapping occurs.

RHYTISMA ANDROMEDAE (Pers.) Fr. on *Andromeda glaucophylla,* from Hope Lake bog, Jefferson Co., July 30, is characterized by profuse production of so-called conidia which are small, hyaline, bacilliform cells, about 4-5 x 1.5 μ. Other Wisconsin specimens do not show this stage, nor do I find it in any of the other collections available for examination.

"RHYTISMA" VITIS Schw. is a tar spot which is fairly common on *Vitis vulpina* in Wisconsin and I have seen it on *Vitis bicolor* (see Davis, Trans. Wis. Acad. Sci. 21: 288. 1924). In a collection made at Lawsonia, Green Lake Co., on *Vitis vulpina*, the conidial stage described by Viala and Sauvageau (Jour. de Bot. 5: 365. 1891) as *Diplodia sclerotiorum* occurs associated with the tar spots. What relation, if any, these forms have to *Pyrenochaeta vitis*, described in the same paper, is not clear to me. When the host epidermis is stripped from the tar spot, coralloid mycelium of the type described for *Pyrenochaeta vitis* is strikingly demonstrated under microscopic examination. So far as I have been able to determine, the tar spots themselves are sterile.

Polygonum sagittatum collected July 30 at Hope Lake, Jefferson Co., bore an immature Ascomycete, apparently parasitic, on its leaves. The ostiolate perithecia, about 75 μ diam., are solitary or few on small spots, 1.5-2 mm. diam., with pale brown center and narrow, deep red border. The asci are well-formed, but spores had not been delimited. It seems possible that this may have some connection with *Sphaeria polygoni-sagittati* Schw. which occurred, however, on dead stems.

RAVENELIA EPIPHYLLA (Schw.) Diet., as evidence presented in an earlier note (Trans. Wis. Acad. Sci. 36: 288. 1944) tended to show, is probably an established member of the Wisconsin fungus flora, and not an impermanent railroad waif. In August 1946 telia of this rust occurred in great abundance on the leaves, petioles, and stems of *Tephrosia virginiana* at Pine Bluff, Dane Co. The old woody stems gave indication of having borne numerous telial pustules the previous season, so it appears possible that the rust overwinters in the crown of this perennial host. Pine Bluff, incidentally, is not adjacent to a railroad.

PHYLLOSTICTA sp., which is probably new, was collected in small quantity, inadequate for a type specimen, on *Osmorhiza claytoni* at Madison, July 8. The dark brown, orbicular spots, 3-8 mm. diam., have a narrow black margin and a paler center. The pale brown pycnidia are gregarious on the spots and are about 100 μ diam., or slightly larger. The hyaline conidia are from 3-3.5 x 4-5 μ. This is a well-marked form, and not one of the *Phyllosticta decidua* complex. There seems to be no previous report of *Phyllosticta* on *Osmorhiza*.

PHYLLOSTICTA on *Arenaria lateriflora* was found in the course of examination of material left by the late J. J. Davis. It was collected at Wyeville, Monroe Co., July 5, 1923, and labeled "*Phyllosticta maricida* n. sp. ad interim" with the following diagnosis: "Spots indefinite, bleached, the surrounding portion and finally the entire leaf becoming light brown and dead; pycnidia globose or sometimes ovoid, brown, the circular ostiole surrounded by a black ring, 70-100 μ diam.; sporules oblong, rounded at the ends, 4-8 x 2-3 μ." Before my discovery of this specimen I had collected this fungus in some abundance at Baxter's Hollow in Sauk Co. and had reported it as *Phyllosticta nebulosa* Sacc., found otherwise on *Silene* in Wisconsin. To me the fungus on *Arenaria* does not seem sufficiently distinctive to warrant its separation as a new species.

ASCOCHYTA LOPHANTHI var. OSMOPHILA Davis (on *Agastache foeniculum*) and *A. lophanthi* var. *lycopina* Davis (on (*Lycopus uniflorus*), as well as a form on *Lycopus americanus,* first recorded as *Ascochyta leonuri* Ell. & Dearn., are grouped under *Ascochyta lophanthi* Davis by him in his *Parasitic Fungi of Wisconsin. A. lophanthi* is described as having spores 20-30 x 10-12 μ, while his specimen on *Lycopus americanus* had spores 8-10 x 4-6 μ. *A. leonuri,* however, was described as with spores 14-17 x 3.5 μ. In a recent collection from Madison on *Lycopus americanus* the spore size is about 20-25 x 7 μ. The wide difference between the two collections on *L. americanus* makes it doubtful that they should be considered identical.

STAGONOSPORA SPARGANII (Fckl.) Sacc. on *Sparganium eurycarpum,* collected at Madison in July, has spores with but a single median septum. However, the ratio of length to width is such that this can scarcely be considered an *Ascochyta. S. sparganii,* like various other sphaeropsidaceous fungi which occur on semi-aquatic hosts, is exceedingly inconspicuous because the pycnidia are developed within the lacunae which are a common feature of such hosts. Thus, the presence of the fungus is indicated only by the dead tissue in the region of attack.

STAGONOSPORA sp. with rather large, thin-walled pycnidia occurred in small amount on the leaves of *Thaspium aureum* at Madison, July 11. The spots are rounded, about 2 mm. diam., with narrow purplish border and pale brown center. The conidia are 10-17 x 3-4 μ, 1-2-septate.

STAGONOSPORA and SEPTORIA, undetermined as to species, have been found on leaves of *Lycium halimifolium* at Madison, August 3. The question of parasitism is complicated by the presence of *Puccinia tumidipes* and *Cercospora lycii* on the leaves. The *Stagonospora* occurs on pale brown, rounded spots, 3-4 mm. diam. The pycnidia are epiphyllous, gregarious, globose, yellow-brown, 115-135 μ diam. The conidia are 3-septate, 20-30 x 3.5-4 μ, slightly to strongly curved. The *Septoria* is on similar spots. The pycnidia are epiphyllous, gregarious, globose, black, 50-65 μ diam. The conidia are somewhat lax, apparently continuous, 20-30 x 1.5 μ.

STAGONOSPORA SIMPLICIOR Sacc. & Berl. is discussed by R. Sprague in *Suppl. 163, Plant Dis. Rep.,* June 15, 1946, entitled *Rootrots and Leafspots of Grains and Grasses in the Northern Great Plains and Western States,* p. 166. He states that this species is for the most part saprophytic. The exception he considers to be a specimen that I determined as *S. simplicior* var. *andropogonis* on *Sorghastrum nutans.* He does not mention a similar, perhaps identical, fungus on *Andropogon furcatus,* which is unquestionably parasitic and has been collected several times in Wisconsin (See Farlowia 1: 575. 1944).

SEPTORIA which occurs commonly on certain species of *Panicum* in Wisconsin, and which I referred to *S. graminum* Desm., cannot be that species, according to R. Sprague, but is better provisionally assigned to *Septoria tandilensis* Speg., where Davis put it.

SEPTORIA PTELEAE Ell. & Ev. on *Ptelea trifoliata* was reported by Davis from Racine, Wis. in 1893. The type was based on this material. Another collection of the same fungus has recently been made in the University of Wisconsin Arboretum at Madison on leaves of planted specimens of the same host. It seems probable to me that this is very close to, if not identical with, *Septoria cirrhosa* Wint. on *Staphylea trifolia*.

SEPTORIA DIVARICATA Ell. & Ev. occurred in good maturity on overwintered green leaves of the repent shoots of *Phlox divaricata* at Oakly, Green Co., May 3, 1947. It would be interesting to know whether the sporules are developed in autumn and are not discharged from the widely ostiolate pycnidia despite vicissitudes of weather, or as seems more likely, are not delimited until the following spring, thus paralleling the behavior of some of the exogenous parasites, which form sterile, sclerotium-like bodies in the fall, and then produce the typical conidia over the surface of the pseudo-sclerotia at the time of the spring rains.

SEPTORIA ATROPURPUREA Peck on *Aster sagittifolius* from Barnes, Bayfield Co., has sporules most of which reach the great length of 165 μ, and some of them even more.

SEPTORIA sp., with pycnidia about 65-80 μ diam. and sporules straight, continuous, about 15-20 x 1 μ, occurs on leaves of a specimen of *Leontodon autumnalis*, collected at Sheboygan by C. Goessl, June 1903. Oudemans does not list any *Septoria* on *Leontodon*, and *Septoria cercosperma* Rostr., reported in Seymour, is a *Rhabdospora*.

COLLETOTRICHUM sp. was found on orbicular brown spots on living leaves of *Smilax ecirrhata*. This is a large species which appears parasitic, but it is perhaps significant that the spots are very similar to those caused by *Stagonospora smilacis*. It seems possible that the *Colletotrichum* is merely secondary, although there is no sign of *Stagonospora* pycnidia.

COLLETOTRICHUM VILLOSUM is described by Weimer (Phytopath. 35: 988. 1945) as occurring on hairy vetch, and on several other species of *Vicia*, including *V. angustifolia*. Weimer considers that this is distinct from *Colletotrichum viciae* Dearn. & Overh. (Mycologia 20: 242. 1928), the principal differences being in the more definite spots and the predominantly hypophyllous acervuli in *C. villosum*. What constiuttes a species is largely a matter of opinion, but it seems to me that this is scarcely more than varietally distinct from *C. viciae*. (Two specimens collected by Davis and this writer in 1935, at Muscoda and Arena respectively, seem to be Weimer's form. These were reported by Davis (Trans. Wis. Acad. Sci. 30: 14. 1937) as *C. viciae*. On the other hand, a collection made by me at Ridgeway in 1943 fits the description of *C. viciae* better than it does that of *C. villosum*. In fact, it corresponds more closely to the original description of *C. viciae* than Overholt's No. 9335 which Weimer cites, and which, so far as the material at Wisconsin is concerned, seems intermediate between *C. viciae* and *C. villosum* as described.)

PUCCINIASTRUM AGRIMONIAE II on *Agrimonia gryposepala,* collected in quantity by Davis in 1918 at Hawkins, Rusk Co., was overgrown by a mucedinaceous fungus. I find that, viewed under a high-powered binocular, it is of identical appearance with *Monosporium uredinicolum* F. L. Stevens, issued as No. 6668 from the Herbarium of the University of Illinois (Porto Rican Fungi) on *Coleosporium ipomoeae.* However, the conidia of the Wisconsin specimen are only about half the size of those of the Porto Rican material. It seems possible that the fungus on *Pucciniastrum* is merely a poor development of *M. uredinicolum.*

DIDYMARIA sp. on *Boltonia asteroides* was collected (but not reported) by Davis at Blue River, Grant Co., August 8, 1922. The specimen is in excellent condition, although scarcely adequate for a type. The conidiophores are so strongly geniculate as to appear tortuous, and are closely clustered in effused hypophyllous patches. They are approximately 75-100 x 3-4 μ. The hyaline, obovate conidia have a median septum, and are 18-23 x 7-8 μ. They appear to be borne in acropleurogenous fashion.

OPHIOCLADIUM HORDEI Cav. is removed from that genus to *Ovularia* by Sprague, as *O. hordei* (Cav.) Sprague (Mycologia 38: 62. 1946). As Sprague notes, this species occurs in Wisconsin on *Phalaris arundinacea.* He considers that the genus *Ophiocladium* is superfluous and should be abolished.

CYLINDROCEPHALUM Bon. on foliage of *Caulophyllum thalictroides* was mentioned in an earlier publication (Trans. Wis. Acad. Sci: 36: 251. 1944). In a recent collection made at Madison on *Hydrophyllum appendiculatum* a similar fungus occurs on large blackened areas on the leaves. The long, tapering, hyaline, several-septate, non-fasciculate conidiophores are up to 120 x 5 μ. The conidia are borne in capitate clusters which separate immediately when mounted for microscopic examination. The conidia are hyaline, cylindrical, 15-20 x 4-5 μ, and some show a median septum which perhaps would bring the organism under *Cephalothecium.* In view of the very ready blackening of the leaves of *Hydrophyllum,* it is questionable that this fungus was the primary agent. *Septocylindrium hydrophylli* Daniels, although microscopically different as described, seems to be an organism of this genre. It likewise occurred on large blackened areas, although the spots were said to be small in the early stages of infection.

RAMULARIA sp., which seems not to be *R. macrospora* or any of its varieties (reported on *Hieracium*) was present in small quantity on leaves of *Hieracium longipilum,* collected at Madison, July 11, 1944. The conidia measured range from 14-23 x 3-3.5 μ, and are continuous or 1-septate; conidiophores 12-15 x 3 μ, hypophyllous.

CERCOSPORA NASTURTII Pass. on *Berteroa incana* was recorded in my *Notes V.* In 1946 a similar fungus was found on the same host at Madison, and a specimen was sent to Chupp who states that he is provisionally regarding *Cercospora berteroae* Hollos as a distinct species, and so assigns the Wisconsin specimen. He points out, however, that the differences between *C.*

nasturtii, C. barbareae, and *C. berteroae* are not very marked, indicating that an alternative taxonomic treatment may ultimately be desirable.

CERCOSPORA sp., collected in small amount on *Hieracium longipilum* at Madison, August 16, 1943, has the following characteristics: Conidia subhyaline, slender, 65-80 x 4 μ, tapering to 2 μ at the tip, indistinctly septate, base truncate, scar prominent; conidiophores 35-55, mostly 35-40 x 4 μ, straight, non-geniculate, with a single very prominent apical scar, pale brown below, fading to a pale gray above, frequently 1-septate, with the septation marking the point of color transition, 5-6 phores in a tuft. Seemingly not *C. hieracii* Ell. & Ev., described as having the phores in dense tufts, 15-20 x 3 μ, and subnodulose, with conidia 50-80 x 2.5-3 μ.

EPICOCCUM NEGLECTUM Desm., ubiquitous as a saprophyte, particularly on dead leaves of grasses, has been found in Wisconsin on a number of occasions developing vigorously on languishing leaves of soy bean, under circumstances which lead one to suspect that it may sometimes be weakly parasitic. F. R. Jones informs me that *E. neglectum* has also been reported on this same host from the Soviet Republic of Georgia.

In an earlier publication (Amer. Midl. Nat. 34: 261. 1945) I mentioned the occurrence of a *Sclerotium*-like non-fruiting fungus on living leaves of *Coreopsis palmata* at Madison. Additional specimens collected in 1945 have, however, large, hyaline, continuous, falcate conidia, mostly about 35 x 3.5-4 μ, borne on the surface of the sclerotia. A specimen was sent to W. C. Snyder to learn whether he considered it to be a *Fusarium*. He states that the lack of septation rules out this possibility. He made a single spore culture of the organism which I have grown on various media, with no definitive results. Large numbers of oval, oidium-like conidia are produced, but the falcate spores have not been formed in culture, nor has a perfect stage been developed.

CERCOSPORA CRASSOIDES J. J. Davis, parasitic on *Froelichia floridana* in Wisconsin, is very likely a species of *Alternaria. Alternaria amaranthi* (Pk.) Hook., likewise on Amaranthaceae, has conidia much smaller than those of *C. crassoides,* which is more similar in size and form to *Alternaria crassa* (Sacc.) Rands which occurs on *Datura.*

ADDITIONAL HOSTS

The fungi mentioned have not been reported as occurring in Wisconsin on the hosts that are cited.

PERONOSPORA TRIFOLIORUM DeBary on *Melilotus alba.* Dane Co., Madison, July 1938. Coll. F. R. Jones & J. G. Dickson.

ERYSIPHE GRAMINIS DC. Conidia only on *Hordeum jubatum,* Dane Co., Madison, July 5. On *Poa compressa,* Sauk Co., Devils Lake, August 5.

ERYSIPHE POLYGONI DC. Conidia only on *Trifolium procumbens.* Dane Co., Paoli, July 15.

ERYSIPHE CICHORACEARUM DC. on *Solidago rigida,* Dane Co., Madison, September 26. On *Aster prenanthoides,* Sauk Co., Parfrey's Glen, October 4. On *Helianthus annuus,* Dane Co., Madison, September 27.

COCCOMYCES sp. *Cylindrosporium* stage on *Prunus nigra.* Lincoln Co., Tomahawk, August 20. So far as I have been able to ascertain there are no other reports of *Coccomyces* on this host, in the case of either natural or artificial infection.

CLAVICEPS NIGRICANS Tul. on *Eleocharis calva.* Washington Co., Cedar Lake, July 23, 1915. Coll. S. Graenicher. On a phanerogamic specimen in the herbarium of the Milwaukee Public Museum.

OPHIODOTHIS HAYDENI (B. & C.) Sacc. on *Aster angustus.* Brown Co., Green Bay, September 1896. Coll. J. H. Schuette. Sterile, as usual. On a phanerogamic specimen in the University of Wisconsin Herbarium.

LOPHODERMIUM PINASTRI (Schrad.) Chev. on *Pinus rigida.* Sauk Co, plantation, 2½ mi. NW of Prairie du Sac, May 7.

EXOBASIDIUM VACCINII (Fckl.) Wor. on *Vaccinium oxycoccos.* Sawyer Co., Hayward, August 21.

AECIDIUM PHYSALIDIS Burr. on *Physalis heterophylla.* Dane Co., Madison, June 8. This appears to be the first collection of this rust in Wisconsin since 1885, when Trelease reported it on *Physalis virginiana.*

PUCCINIA ASPARAGI DC. on *Allium cepa bulbifera* is reported in *Arthur's Manual* from Wisconsin. Davis did not record this in his notes, nor is there a specimen in the herbarium. However, G. B. Cummins informs me that there are two aecial specimens in the Arthur Herbarium, both from Madison, one collected June 16, 1919 by A. L. Gates, the other July 3, 1920 by J. C. Walker.

PUCCINIA EXTENSICOLA Plowr. III on *Carex adusta* Boott. Bayfield Co., Drummond, June 29, 1896. Coll. L. S. Cheney. Host det. confirmed by K. Mackenzie. On previous year's leaves still attached to a phanerogamic specimen in the University of Wisconsin Herbarium.

UROMYCES MINUTUS Diet. III on *Carex pubescens.* Price Co., Camp Merrill near Phillips, September 19, 1911. Coll. J. J. Davis. Davis failed to place this specimen in the herbarium, although it is well marked, both as to host and parasite.

USTILAGO BULLATA Berk. on *Bromus inermis,* Dane Co., Madison, University Hill Farm, July 23, 1945. On *Bromus erectus,* Waushara Co., Hancock, Experimental Station Grass Nursery, July 10, 1946. Both specimens coll. & det. by J. G. Dickson.

PHYLLOSTICTA MONARDAE Ell. & Barth. on *Mentha arvensis* var. *canadensis.* Dane Co., Madison, July 25. This is quite different from *Phyllosticta*

decidua Ell. & Kell. which has been reported on a number of species of *Mentha*.

PHYLLOSTICTA DECIDUA Ell. & Kell. on *Valeriana officinalis*. Dane Co., Madison, July 12.

PHYLLOSTICTA CIRSII Desm. on *Cirsium undulatum*. Dane Co., Madison, August 9. Principally on leaves of first-year rosettes.

ASCOCHYTA GRAMINICOLA Sacc. on *Panicum capillare*. Dane Co., Madison, September 15. The conidia are about 14-16 x 3-4 μ. A specimen was sent to Sprague who states that the fungus appears to be in the *A. graminicola* group, close to var. *holci* Sacc.

ASCOCHYTA PISI Lib. on *Lathyrus venosus* var. *intonsus*. Dane Co., Madison, July 24. Davis in his *Parasitic Fungi of Wisconsin*, p. 71, mentions finding pycnidia containing spores of the *Ascochyta pisi* type on spots bearing *Cercospora viicae* on this host, but he did not enter a specimen in the herbarium. In the present collection the light-colored pycnidia, 150 μ or more in diam., are borne on indefinite pale brown spots, involving the leaf margin.

DARLUCA FLIUM (Biv.) Cast. on *Puccinia asteris* on *Aster oblongifolius* var. *angustatus*. Columbia Co., Black Hawk's Lookout, near Prairie du Sac, August 5, 1922. Coll. Huron H. Smith.

STAGONOSPORA ZONATA J. J. Davis on *Asclepias tuberosa*, Sauk Co., Cactus Bluff, Town of Prairie du Sac, August 23. On *Asclepias incarnata*, Dane Co., Madison, September 20, 1945, and on the same host a specimen, collected and determined by Davis, from Arcadia, Trempeleau Co., September 4, 1917. Davis apparently overlooked the Arcadia collection, for I find no record of it in his writings. The lesions produced are similar to those on *Asclepias incarnata* caused by *Septoria asclepiadicola* Ell. & Ev. In the two recent collections the conidia are up to twice the 12-25 μ length of the original description, yet the lesions seem very characteristic. The collection on which the type is based may be somewhat immature.

SEPTORIA RUMICICOLA Allesch. (or *S. rumicis* Trail ?) on *Rumex altissimus*. Iowa Co., Arena, May 21. Earlier reports of *Septoria* on this host in Wisconsin apparently refer to *Rumex mexicanus*.

SEPTORIA RHOINA B. & C. on *Rhus copallina*. Columbia Co., Lodi, August 6.

SEPTORIA OENOTHERAE West. on *Gaura biennis*. Vernon Co., Genoa, August 23. Apparently the first report of this species on *Gaura*. *Septoria gaurina* Ell. & Kell. has much thicker and more strongly curved sporules.

SEPTORIA LYSIMACHIAE West. on *Lysimachia thrysiflora*. Dane Co., Madison, July 25. Also found on the leaves of a phanerogamic specimen of *Lysimachia nummularia* from Arena, Iowa Co., June 21, 1937. Coll. F. J. Hermann. The sporules of the specimen on *L. thyrsiflora* are about 35 μ, rather than the 50 μ of the description.

SEPTORIA INCONSPICUA B. & C. on *Plantago major*. Jefferson Co., Hope Lake, July 30. On the authority of Trelease, Davis reports *Septoria plantaginis* (Ces.) Sacc. on *Plantago major* in Wisconsin, but the species is not mentioned in Trelease's list. I have reached the conclusion that all specimens of *Septoria* collected by me on *Plantago* in Wisconsin should be referred to *S. inconspicua*. This includes specimens on *P. aristata* and *P. purshii* which I have previously reported as *S. plantaginea* Pass. var. *plantaginis-majoris* Sacc. Also found on *Plantago rugelii* at Madison, August 30. Here the spots are rounded, rather large, ashen, with many pycnidia per spot. As in other specimens the pycnidia are rostrate.

SEPTORIA FUMOSA Peck on *Solidago rigida*. Columbia Co., Black Hawk's Lookout near Prairie du Sac, August 12. This is assigned here principally on the basis of microscopic characters. The spots are very small, angled, and dull purplish. Most of the sporules are slightly less than 50 μ long.

SEPTORIA ASTERICOLA Ell. & Ev. on *Aster prenanthoides*. Sauk Co., Devil's Lake, July 6. On this host the broad yellow borders of the spots, mentioned in the original description of the fungus on *Aster cordifolius*, are not very strongly marked, but microscopic agreement is good. Most of the slender sporules are about 30 μ long. The dark purple spots are reminiscent of *Septoria atropurpurea* Peck, but the short narrow sporules are very different. *S. solidaginicola* Peck, likewise occurring on *Aster*, has short sporules, but they are described as being up to 4 μ wide, in contrast to the very slender, filiform ones of this specimen.

DILOPHOSPORA ALOPECURI Fr. on *Phalaris arundinacea*. Dane Co., Madison, July 31. This curious fungus has not been reported before on *Phalaris*, so far as I have been able to determine.

COLLETOTRICHUM VIOLAE-ROTUNDIFOLIAE (Sacc.) House on *Viola pedata*. Dane Co., Madison, October 8.

COLLETOTRICHUM SOLITARIUM Ell. & Barth. on *Solidago sciaphila*. Sauk Co., Cactus Bluff, Town of Prairie du Sac, August 23.

TITAEOSPORA DETOSPORA (Sacc.) Bub. on *Equisetum arvense*, Columbia Co., Lodi, August 6. On *Equisetum hyemale*, Sauk Co., Parfrey's Glen, July 27. The latter specimen collected by M. E. Hoppe. This is supposed to be the conidial stage of *Stamnaria*, and occurred on plants which later developed the perfect condition.

RAMULARIA ANOMALA Peck on *Polygonum punctatum*. Columbia Co., Lodi, September 16. There are no spots on the leaf. The fungus is in rounded patches, indicating equal radial growth outward from a center of infection. The host was growing in close proximity to *Polygonum scandens* infected with the same parasite. On *Polygonum persicaria*, Dane Co., Madison, September 21. Davis (Trans. Wis. Acad. Sci. 20: 415. 1922) discusses the relationships of species of *Ramularia* on *Polygonum* at some length and states concerning a collection on *P. persicaria* "In August 1920 there was

collected in small quantity at Chaseburg a *Ramularia* on *Polygonum Persicaria* in which the areas bearing the tufts are not at first discolored but become pale brown, the discoloration showing more plainly after the leaf is dried. The conidia are but 1-1½ μ thick. It is quite likely that the forms on *Persicaria, Tiniaria,* and *Fagopyrum* will prove to be distinct in their host relations." The Madison collection has conidia about 3 μ thick and meets the morphological specifications of *R. anomala* so is, for the present at least, assigned to that species.

RAMULARIA VIRGAUREAE Thum. on *Solidago sciaphila.* Columbia Co., Black Hawk's Lookout near Prairie du Sac, September 10. This is a slender and almost depauperate form, similar to a collection Davis once made on *Solidago serotina* (Trans. Wis. Acad. Sci. 21: 259. 1924).

CERCOSPORELLA NIVEA Ell. & Barth. on *Solidago speciosa.* Columbia Co., Black Hawk's Lookout near Prairie du Sac, August 12. The strongly tapered obclavate conidia, up to 125 x 4 μ or more, are absolutely not suggestive of *Ramularia* as I understand it, and I fail to see how forms of this type can be assigned, as they sometimes have been, to *Ramularia virgaureae* Thum.

CLADOSPORIUM AROMATICUM Ell. & Ev. on *Rhus copallina.* Columbia Co., Lodi, August 6. Not listed by Seymour on this host.

SCOLECOTRICHUM GRAMINIS Fckl. on *Poa palustris,* Dane Co., Madison, July 16. On *Glyceria borealis,* Madison, July 8.

HELMINTHOSPORIUM BROMI Died. on *Bromus japonicus.* Dane Co., Madison, July 22.

CERCOSPORA CARICINA Ell. & Dearn. on *Carex stipata,* Dane Co., Madison, July 25. On *Carex muhlenbergii,* Columbia Co., Lodi, September 16.

CERCOSPORA ZIZAE Ell. & Ev. on *Zizia aptera* (*cordata*). Waukesha Co., Scuppernong Prairie near Eagle, July 19.

CERCOSPORA LITHOSPERMI Chupp & Greene on *Lithospermum canescens.* St. Croix Co., Hudson, Hudson, August 22. Some of the acicular conidia measure as much as 200 μ, much greater than the length given in the description, based on material on *Lithospermum croceum.* Nevertheless, in type of spot, conidiophores, and shape of conidia, the specimen is characteristic. Also collected on this host at Madison, Dane Co., September 12.

CERCOSPORA PLANTAGINIS Sacc. on *Plantago rugelii.* Dane Co., Madison, August 16, 1943.

CERCOSPORA GNAPHALIACEA Cke. on *Gnaphalium uliginosum.* Douglas Co., T 46 N R 11 W (south of Lake Nebagamon), September 4, 1942. Coll. J. W. Thomson. Record from a heavily infected phanerogamic specimen in the University of Wisconsin Herbarium. Seemingly the first report of *Cercospora* on this host.

ALTERNARIA BRASSICAE (Berk.) Sacc. on *Lepidium campestre*. Dane Co., Madison, July 16. Peck described this as *Cercospora lepidii*. Chupp and Pirone (Plant Dis. Rep. 19: 275. 1935) pointed out the identity with *A. brassicae*. Also on *Raphanus sativus* at Madison, October 8.

ALTERNARIA SOLANI (E. & M.) Jones & Grout on *Solanum melongena*. Dane Co., Madison, October 8.

ADDITIONAL SPECIES

The fungi mentioned have not previously been reported to occur in Wisconsin.

CHOANEPHORA CUCURBITARUM (B. & Rav.) Thax. on flowers and fruits of *Cucurbita pepo* (pumpkin). Dane Co., Madison, September 6. Coll. & det. C. W. Hesseltine.

PERONOSPORA TABACINA Adam on *Nicotiana tabacum*. Dane Co., Madison, University of Wisconsin Hill Farm, September 25. Coll. H. E. Heggestad. Det. C. G. Shaw. A dangerous parasite.

PERONOSPORA PLANTAGINIS Underw. on *Plantago aristata* and *Plantago purshii*. C. G. Shaw, who has made a special study of the Peronosporaceae of Wisconsin, finds that the fungus reported in my notes as *Peronospora alta* Fckl. is *P. plantaginis*, previously unreported in Wisconsin.

CATACAUMA FLABELLUM (Schw.) Theiss. & Syd. on *Pteridium aquilinum* var. *latiusculum*. Sauk Co., Cactus Bluff, Town of Prairie du Sac, August 23. Immature, but conidia were found, most of the cells of which are about 12-14 x 1.5 μ and continuous. They are hyaline. The conidia failed to germinate in tap water after 48 hours, which may indicate that they are not truly functional. In this connection Orton's statement (Mycologia 16: 90. 1924) is of interest: "*Catacauma flabellum* appears to be a highly specialized but much reduced type of parasitic Pyrenomycete in which not only has a reduction in the perithecium taken place but the conidial stage has entirely disappeared."

MYCOSPHAERELLA LYCOPODII (Pk.) House on *Lycopodium obscurum* var. *dendroideum*. Sawyer Co., Hayward, August 21. Dubiously parasitic. The major portions of the infected plants were green and healthy, but the leaves on which the fungus occurred were dead.

LOPHODERMIUM DURILABRUM Darker on *Pinus strobus*. Jackson Co., Black River Falls, July 1, 1916. Coll. J. J. Davis. Det. G. D. Darker, 1946. The specimen was originally determined as *Lophodermium pinastri*. Darker also finds *Hypoderma desmazierii* present.

LOPHODERMIUM NITENS Darker on *Pinus strobus*. Door Co., Fish Creek, July 2, 1919; Washington Island, July 1, 1931; Sheboygan Co., Sheboygan, July 2, 1935; Sauk Co., Baxter's Hollow, Town of Sumpter, March 26, 1938; Dane Co., Madison, May 21, 1943. All these were first determined as *L.*

pinastri, but, according to Darker's findings, the latter species has not yet been collected on *Pinus strobus* in Wisconsin.

SPHACELOTHECA OCCIDENTALIS G. P. Clint. on *Andropogon furcatus*. Dane Co., Madison, September 9, 1946. A striking species, with columella and peridium strongly developed.

PHYLLOSTICTA CANNABIS (Kirchn.) Speg. on *Cannabis sativa*. Dane Co., Madison, September 26. This corresponds exactly with No. 601 of Kabat and Bubak's "Fungi imperfecti exsiccati," issued as this species.

PHYLLOSTICTA FRAGARICOLA Desm. & Rob. on *Potentilla arguta*. Dane Co., Madison, August 19, 1945. Referred here with doubt. The species is seemingly widespread in Europe on cultivated strawberry. The microscopic characters are in good agreement. On *P. arguta* the epiphyllous pycnidia are sparsely distributed on reddish orbicular spots which range from 2-6 mm. diam. Some of the smaller spots have a decided purplish tinge and all have a sharply defined narrow margin. The pycnidia are mostly about 100-150 μ diam., rather imperfectly developed below and widely ostiolate, so that in many cases the conidial masses are prominently extruded.

Phyllosticta physocarpi sp. nov.

Maculis suborbicularibus, 2-10 mm. diam., marginibus fuscis, centris cinereis, infra brunneis obscuris; pycnidiis epiphyllis, prope superficialibus, gregariis, fumidus, pseudoparenchymaticis, subglobosis, ostiolatis, 100-150 μ diam.; conidiis hyalinis, ellipsoideis vel subfusoideis, 5-7 x 3-4 μ.

Spots suborbicular, 2-10 mm. diam., border blackish-brown, center cinereous, dull brown below; pycnidia epiphyllous, almost superficial, gregarious, sooty pseudoparenchymatous, subglobose, ostiolate, 100-150 μ diam.; conidia hyaline, ellipsoid or subfusoid, 5-7 x 3-4 μ.

On living leaves of *Physocarpus opulifolius*. Columbia County, Black Hawk's Lookout near Prairie du Sac, Wisconsin, U. S. A., August 12, 1946.

PHYLLOSTICTA SOLITARIA Ell. & Ev. on fruit of *X Pyrus prunifolia*. Dane Co., Madison, July 22. On leaves of the same tree, August 30. The aptness of the specific name is evident when one observes the tiny and uniformly dispersed leaf lesions, each with a solitary pycnidium.

PHYLLOSTICTA STAPHYLEAE Dearn. on *Staphylea trifolia*. Green Co., Brodhead, June 7. This specimen occurred on the leaves of a non-flowering shoot, while the type was on the mature pods. Nevertheless, it corresponds well. In the Wisconsin specimen the spores are perhaps slightly more rotund, but all have a decidedly smoky tinge, which seems characteristic of the species.

PHYLLOSTICTA HIERACII Allesch. on *Hieracium longipilum*. Dane Co., Madison, September 3. In most respects this conforms quite closely to the description. In the specimen on *H. longipilum* the biguttulate conidia are ca. 6-9 x 2.5-3 μ, instead of the 4-7 x 2-3 μ of the description, and the pycnidia

are brown instead of black. The large rounded or ellipsoid spots, which frequently impinge on the leaf margin, are 1-2 cm. diam., grayish-brown with narrow red borders.

PHOMA MARIAE Clint. on living stems of *Lonicera* sp. (cult.). Racine Co., June 1894. F. L. Stevens (North American Fungi, 2nd series, No. 3157). Described by Clinton as developing on living stems of *Lonicera flava* and *L. tatarica*. Since this is evidently a parasite it is tardily recorded, despite the fact that Davis did not see fit to mention it in his notes.

DIPLODINA DESTRUCTIVA (Plowr.) Petr. on fruit of *Lycopersicum esculentum*. Dane Co., Madison, September 7. Coll. and det. C. W. Hesseltine.

DIPLODIA THALICTRI Ell. & Dearn. on *Thalictrum dasycarpum*. Dane Co., Madison, September 1, 1944. This occurred on living leaves, whereas Ellis and Dearness described the species from dead stems of *Thalictrum polygamum*. The following notes were made on the Wisconsin specimen: Spots small, mostly 1-3 mm. diam., rounded or angled, or somewhat elongate, gray-brown with narrow, raised, fuscous borders; pycnidia epiphyllous, gregarious, or only one to a spot on the smallest lesions, blackish, octiolate, subglobose, 125-175 μ diam. approx.; conidia short-cylindric or ovate, uniseptate, pale brown, 12-14 x 4-6 μ. The spots, particularly on their under side, are reminiscent of old lesions of *Cylindrosporium thalictri*, but scrapings from a number of them failed to yield any *Cylindrosporium* conidia.

SEPTORIA SPARTINAE (Trel.) Sprague is the new combination made by Sprague (Septoria Diseases of Gramineae in Western United States. Ore. State Coll. Monogr. Studies in Bot. 6: 131. 1944) for the organism on *Spartina pectinata*, described by Trelease as *Ascochyta spartinae* (Trans. Wis. Acad. Sci. 5: 121. 1885).

SEPTORIA MACROPODA Pass. var. SEPTULATA (Gonz. Frag.) Sprague on *Poa pratensis*. Dane Co., Madison, November 8, 1921. Coll. G. F. Weber. Weber did not determine this, but reported it only as *Septoria* sp., and Davis followed him in this. Sprague, in his monograph on the graminicolous Septorias, discusses *S. macropoda* and its varieties in detail.

SEPTORIA WALDSTEINIAE Pk. & Cl. on *Waldsteinia fragarioides*. Bayfield Co., Barnes, August 21. Unfortunately the specimen on which this report is based has been lost, but I feel justified in recording it since I personally collected and examined the material.

SEPTORIA EXOTICA Speg. on *Veronica spicata* (cult.). Dane Co., Madison, August 4. In the well-marked spots, with arid centers, and in the short, rather lax sporules, this specimen corresponds quite closely with that of *S. exotica* on *Veronica elliptica*, issued as No. 64 of Kabat and Bubak's *Fungi imperfecti exsiccati*.

SEPTORIA MACROSPORIA Dearn. on *Chrysanthemum leucanthemum* (cult.). Dane Co., Madison, August 17. The sporules are almost linear, up to 100 x

3.5-4 μ, and the pycnidia are well-developed. Otherwise it is close to *Cylindrosporium chrysanthemi* Ell. & Dearn.

SELENOPHOMA DONACIS var. STOMATICOLA (Bauml.) Sprague & Johnson on *Sporobolus heterolepis*. Dane Co., near Sauk City, September 18. Det. R. Sprague (see Mycologia 37: 639. 1945). According to Sprague this fungus is common on *Sporobolus cryptandrus* and *S. asper* in the Northwest, but this is the first specimen on *S. heterolepis* that he has seen.

PHLYCTAENA LINICOLA Speg. on *Linum usitatissimum*. Dane Co., Madison, August 15, 1941. Coll. G. A. Gries.

COLLETOTRICHUM PHOMOIDES (Sacc.) Cnester is reported on *Lycopersicum esculentum* from Madison by Kendrick (Phytopath. 37: 12. 1947). He finds that the fungus overwinters in tomato refuse, i. e., dead stems and petioles.

CYLINDROSPORIUM CHRYSANTHEMI Ell. & Dearn. on *Chrysanthemum* sp. (cult.). Dane Co., Madison, October 20, 1944. The host is probably either *Chrysanthemum indicum* or *C. morifolium*. *Cylindrosporium chrysanthemi* seems to differ from *Septoria macrosporia* Dearn. principally in the very noticeably tapered spores, which are about 3.5 μ at the base. If this is a good *Cylindrosporium*, it seems very probable that the name *Septoria obesa* Syd. is a synonym.

CERCOSPORA SYMPHORICARPI Ell. & Ev. on *Symphoricarpos albus* var. *laevigatus*. Bayfield Co., Barnes, August 21.

ISARIOPSIS GRISEOLA Sacc. on *Phaseolus vulgaris*. Dane Co., Madison, September 15. Coll. J. C. Walker. The rounded spots are numerous and sharply delimited. This appears to be a virulent parasite.

Notes on Wisconsin Parasitic Fungi. XIII.

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The collections of fungi referred to in this series of notes were made, unless indicated otherwise, in the season of 1948.

Powdery mildews, undetermined as to species, occurred on the following hosts, not before reported as bearing this class of fungi in Wisconsin: *Fragaria virginiana,* Dane Co., Madison, June 24; *Onosmodium molle* var. *occidentale,* Green Co., Town of York, Sect. 3, July 24; *Blephilia ciliata,* Madison, June 29; *Senecio balsamitae,* Madison, July 4.

VENTURIA CLINTONII Peck, in good maturity, occurred on fallen leaves of *Cornus rugosa* (*circinata*) at Sturgeon Bay, Door Co., April 23. Coll. J. S. Boyle. The upper leaf surface has rounded, black, stromatoid patches, while most of the perithecia are hypophyllous and concentrated below the patches, but by no means closely confined to them. Cultures from ascopores were made, but no conidia were produced. So far as I am aware this has not yet been connected with a parasitic imperfect stage. Also collected at Cactus Bluff, Town of Prairie du Sac, Sauk Co., May 7.

MYCOSPHAERELLA sp. developed on the current season's basal leaves of *Hystrix patula* near Brooklyn, Green Co. Since the leaves were brown and dead when observed, it is uncertain whether the fungus is a parasite. The subglobose perithecia, about 65-75 μ diam., are closely crowded on elongate lesions. The clavate asci are about 35 x 10 μ, the uniseptate ascospores 13 x 4 μ.

MYCOSPHAERELLA sp., on living leaves of *Polygonum sagittatum,* Madison, July 22, is tentatively referred to *Sphaerella rumicis* (Desm.) Cke. to which it corresponds more closely in dimensions than to *Sphaerella polygonorum* (Crie) Sacc. However, specimens of *S. rumicis* on *Rumex* from the West Coast differ in type of spot and in having spores with a greenish tinge, whereas the Madison specimen has hyaline spores, attributable perhaps to immaturity. On *Polygonum sagittatum* the perithecia are scattered over rather large, angled, dead areas. On *Rumex* they are closely clustered on small, round spots. An immature Ascomycete, probably a *Mycosphaerella,* collected on *P. sagittatum* in 1946 in Jefferson Co., does occur on small round spots.

USTILAGO OXALIDIS Ell. & Tracy on *Oxalis stricta.* Dane Co., Madison, June 18, 1943. Overlooked on plants that were collected for the *Phyllosticta* that they bore. The first Wisconsin specimen in the University Herbarium, although Davis recorded it as occurring in the state on the basis of a report in Clinton's list of North American smuts.

"USTILAGO" OSMUNDAE Peck on *Osmunda regalis* has been found in Wisconsin and at various stations in the eastern United States. The systematic position of this fungus has been questioned by various authors, including G. P. Clinton, but no definitive study has yet been made. In 1912 L. D. Bagely, in a University of Wisconsin Bachelor's thesis, entitled *A Cytological Study of Ustilago osmundae Pk. on Osmunda regalis L.*, reached the conclusion that the fungus has the essential characteristics of *Ustilago* and is therefore probably correctly placed there. However, Bagely was unable to germinate the spores. J. A. Stevenson informs me that very recently this problem has come to the notice of his Division and that Dr. Lee Ling took a fresh specimen of *U. osmundae* and was successful in germinating the spores and studying their development. He is of the opinion that this is not a true smut.

UROCYSTIS AGROPYRI (Preuss) Schroet. is reported on *Phleum pratense* by Kreitlow (Phytopath. 38: 158. 1948). His specimens are from two northeastern stations, but he also cites an unreported specimen of Drechsler's from Warrensburg, Mo. It appears that this smut should be looked for on timothy in Wisconsin.

PUCCINIA HIERACII (Schum.) Mart. is one of the rusts which have so-called uredinoid aecia. That the sori are more uredial than aecial is perhaps indicated by the fact that I have on several occasions observed them being parasitized by *Darluca filum* which rarely attacks ordinary aecia.

PHYLLOSTICTA sp. which seems morphologically identical with *Ph. paviae* Desm., attacking *Aesculus*, occurred at Madison on leaves of *Thuja occidentalis*. The conidia are noteworthy in having a shadowy hyaline appendage. A specimen was sent to Glenn G. Hahn who called to my attention a paper by V. B. Stewart (Phytopath. 6: 10. 1916) dealing with the leaf blotch disease of horse chestnut. The causal agent is *Guignardia aesculi* (Peck) Stewart whose conidial stage, *Ph. paviae*, produces the leaf lesions. Since this organism is definitely a parasite it seems highly improbable that it carries over to *Thuja*, but on the basis of morphology alone one would reach that conclusion.

PHYLLOSTICTAE which occur on *Polygonatum, Smilacina, Oakesia,* and *Uvularia* have been a source of confusion because of their considerable variability. So far as Wisconsin material is concerned, I am at present separating these forms as follows: 1) Spores hyaline, elongate—*Phyllosticta cruenta* (Fr.) Kx. on *Polygonatum, Uvularia,* and *Oakesia;* 2) Spores hyaline, globose, a) about 10 μ diam.—*Phyllosticta pallidior* Peck on *Smilacina,* b) about 5-7 μ diam.—*Phyllosticta discincta* J. J. Davis on *Uvularia;* 3) Spores brown, elongate—*Diplodia uvulariae* J. J. Davis on *Oakesia,* and doubtfully on *Uvularia.* A large collection of *Ph. discincta,* from the New Glarus Woods, Green Co., has spots which are small, angular, arid and very sharply delimited, in contrast to the rather diffuse spots of other collections of this species. It is perhaps varietally distinct. I am inclined to consider that *Ph. oakesiae* Dearn. & House is synonymous with *Ph. cruenta,* and that *Ph. convallariae* Pers., as

treated by Seaver, contains more than a single entity. Davis places together the small-spored globose form on *Uvularia* and the elongate-spored forms on *Uvularia* and *Oakesia*, under the name *Ph. cruenta* var. *discincta* Davis, but I feel that the small-spored form is much better segregated.

PHYLLOSTICTAE of diverse microscopic character occur on galls of *Taphrina caerulescens* on *Quercus rubra*, collected near Brodhead, Green Co., July 28. One specimen has very large conidia of the *Macrophoma* type, while in others the conidia are quite small. None corresponds with *Phoma parasitica* Ell. & Ev., said to be parasitic on *Taphrina*. I am uncertain as to the parasitism of the forms that I have seen.

PHYLLOSTICTA GROSSULARIAE Sacc. was reported by Ellis and Everhart on *Ribes americanum* from Wisconsin, but there was no specimen in the University Herbarium. A recent collection from Madison on this host is referred with some doubt to *Ph. grossulariae*. The epiphyllous pycnidia are flesh-colored and, except for their small size, are of the type that I have come to associate with *Ascochyta*. There is, however, no evidence of septation in any of the spores. The spots are rounded to fusoid, with pale brown centers and rather wide dark margins.

PHYLLOSTICTA on *Tropaeolum majus*, Madison, July 11, is perhaps *Ph. tropaeoli* Sacc. & Speg. Correspondence in microscopic characters is close, but the fungus is on arid, lobed lesions, whereas *Ph. tropaeoli* is said not to produce spots.

ASCHOCHYTA SPARTINAE Trel. has been transferred to *Septoria* by Sprague, and seemingly quite properly so, but I have recently found near Brodhead, Green Co., a very well-defined species of *Ascochyta* on living leaves of *Spartina pectinata*. The elongate spots, 3 x 1 mm., are dull brown and the rather large, thin-walled pycnidia are epiphyllous. The conidia are 8-12 x 3-4 μ, clearly and consistently 1-septate. The specimen is too small to serve as a type.

ASCOCHYTA sp. occurs in small amount on a green leaf of a phanerogamic specimen of *Sullivantia renifolia*, collected by N. C. Fassett at Wilton, Monroe Co., July 1932. The tan spots with narrow, raised, purplish border are marginal, about 1 cm. wide. The pycnidia are scattered, about 200 μ diam., the conidia 10-14 x 3-4 μ. I do not find any reports of fungi on *Sullivantia*.

ASCOCHYTA THASPII Ell. & Ev. on *Sanicula marilandica*, Madison, July 19, is restricted to small, sharply delimited ashen spots, in contrast to the one earlier Wisconsin specimen on this host, where the pycnidia are scattered over discolored areas of large and indefinite extent.

ASCOCHYTA sp. on *Senecio balsamitae*, Madison, June 19, is epiphyllous on very small, bleached spots, which are irregularly rounded, with a narrow, raised, blackish margin. There are only one or two pycnidia per spot. They are globose, sooty-olivaceous, about 100 μ diam. The hyaline conidia are up

to 17 x 3 μ. Not far from *Stagonospora*, but no conidia with more than one septum were observed.

DARLUCA FILUM (Biv.) Cast. occurred on aecia of *Puccinia extensicola* Plowr. on *Aster oblongifolius* var. *angustatus* in Columbia Co., near Prairie du Sac, May 7. *Darluca* is usually found in the uredial sori of various rusts, and occasionally in the telia. I have never before, in an extensive collecting experience, found *Darluca* on *Aecidium* and, judging by the lone specimen (not from Wisconsin) in our herbarium, such development must be highly unusual.

DAVISIELLA ELYMINA (Davis) Petrak was considered by Petrak (Ann. Mycol. 22: 133. 1924) to be a sphaeropsidaceous fungus, parasitic in the locules of *Phyllachora* on Gramineae. Davis described the fungus as *Cytodiplospora elymina*, regarding it as a spermogonial stage of *Phyllachora*. I am inclined to wonder whether its association with *Phyllachora* may not be accidental, and due to the overgrowth of the pycnidia by the *Phyllachora*, much as one of the larger fungi will sometimes overrun and include part of its substratum. I have recently observed pycnidia of the *Davisiella* type on leaves of *Hystrix patula* and *Elymus villosus*. These leaves do not show any *Phyllachora*, but *Hystrix*, particularly, almost always has a heavy infection later in the season. An examination of the type of *Cytodiplospora elymina* reveals numerous pycnidia with 2-3-septate conidia, entirely free of the *Phyllachora* ascomata, and closely resembling the recent specimens collected by me. Davis described the conidia as 1-septate, but later collections have 2-3-septate conidia in pycnidia enclosed by the *Phyllachora*.

STAGONOSPORA sp. which I am unable to assign occurred on the still green overwintered leaves of *Carex albursina* (*C. laxiflora* var. *latifolia*) near Albany, Green Co., May 8. The spores are quite uniformly 35 x 6-7 μ, while *S. caricis* (Oud.) Sacc. is stated to have spores 25-40 x 4-5 μ.

STAGONOSPORA sp., in quantity inadequate for a type specimen, occurred on leaves of *Sium suave* near Monticello, Green Co., July 28. The spots are small, angled, white, 1-1.5 mm. The sparse pycnidia are sooty, 100 μ or somewhat more in diameter. The conidia are subfusoid to cylindric, 1-, 2-, or 3-septate, 12-18 x 3.5-5 μ.

SEPTORIA sp. was found on leaves of *Maianthemum canadense* from Otsego, Columbia Co., July 10. This does not correspond with other species of *Septoria* reported on *Maianthemum* or other closely related plants. This seems to be new, but the specimen is not large enough to serve as a satisfactory type. The spots are 8-10 mm. long x 4-5 mm. wide, pale brown with narrow red border, and with an additional yellow halo about the entire spot. The globose pycnidia are olivaceous, pseudoparenchymatous, rather widely ostiolate, 65-85 μ diam. The conidia are small and slender, 15-30 x 1-1.5 μ, hyaline and continuous. *Septoria maianthemi* West. has conidia 50-70 x 3 μ. *Septoria streptopidis* Peck is cited in Seymour's Index as occurring on *Streptopus roseus* and it seemed possible that the Wisconsin fungus might be that

species. However, H. D. House informs me that he has seen no specimens and does not think that Peck published this species. He is at a loss to account for the mention of it by Seymour.

SEPTORIA sp. occurred on small, rounded, brown spots on a leaf of *Habenaria leucophaea* collected at Madison, July 21. The epiphyllous pycnidia are pale olivaceous, except for a conspicuous ring of sooty cells around the ostiole, subglobose, about 150 μ diam. The conidia are hyaline, continuous, 15-30 x 2-3 μ, obtuse at one end, tapered at the other.

SEPTORIA RUMICIS Trail occurs on *Rumex* in Wisconsin, if width of sporules is considered significant. In a specimen on *Rumex verticillatus* from Blue River, Grant Co., the conidia are about 25-35 x 2-2.5 μ, and 1-septate, roughly the size range of Trail's species. Specimens on other species of *Rumex*, collected by Davis, have similar or even somewhat larger conidia. On the other hand, *S. rumicis* Ell. (described after Trail's species) and *S. rumicicola* Allesch. are stated to have conidia 15-25 x 1.5-2 μ and are evidently identical. Sydow's Mycotheca Germanica No. 3167, distributed as *S. rumicis* Trail, has conidia which are 3-septate and as wide or wider than Wisconsin specimens. In the absence of type material for comparative study it seems advisable to consider *S. rumicis* Trail and *S. rumicicola* Allesch. as entities, for the time being. The *Septoria* on *Rumex* in Wisconsin seems to be all the same thing, and I am assigning it to *S. rumicis* Trail.

SEPTORIA HEPATICAE Desm., as it develops on species of *Hepatica* in Wisconsin, is perhaps only weakly parasitic. It is usually on leaves which have been attacked primarily by some other fungus, or on overwintered leaves.

SEPTORIA BACILLIGERA Wint, had infected all the cotyledonary leaves of small plants of *Ambrosia trifida* in a large patch of this weed at Milford, Jefferson Co., May 15. Foliage leaves were not infected at this date, but the fallen cotyledonary leaves no doubt provide a source of inoculum throughout the growing season. A graphic example of seed-borne infection in an annual host.

COLLETOTRICHUM PECKII (Sacc.) Davis on *Trillium recurvatum*, Town of Spring Grove, Green Co., May 1, appears to be parasitic on well-defined spots on leaves of vigorously growing plants. Davis made an earlier collection on this host, but in that instance the plant was in poor condition, and to him it seemed probable that the fungus had developed saprophytically.

OVULARIA PYROLAE Trel. has been represented in the University of Wisconsin Herbarium by a single small specimen on *Pyrola elliptica*, collected by Davis at Manitowish, Iron Co., in 1910. An ample specimen of the same thing on the same host has recently been taken near Verona, Dane Co. As indicated in the description, the lesions are dark and rounded. In section masses of conidia are seen to be produced on sporodochia which have originated subepidermally. To me this is reminiscent of the reduced stage of a *Fusarium*, but I find no typical macroconidia at all, and none of the conidia

are septate. In the Verona specimen most of the fruiting is located along the veins. The fungus in question surely does not belong in the Moniliaceae. Davis examined the type specimen and stated in a letter to Trelease "My small specimen on *Pyrola elliptica* with its thinner, softer, smaller leaves differs only in the affected areas being larger and less definitely circumscribed."

CERCOSPORELLA SAXIFRAGAE Rostr., on *Saxifraga pennsylvanica*, like some other similar fungi, persists over winter in a sclerotoid state on the leaves of the basal rosette. Following spring rains, fresh conidia are produced from the sclerotium-like bodies in close proximity to newly formed leaves of the current season, thus probably facilitating their early infection.

RHIZOCTONIA stolon rot of Ladino clover (*Trifolium repens*) has been found by J. G. Dickson in plots at the University of Wisconsin Experimental Farm at Hancock, Waushara Co.

Psoralea esculenta seedlings in a University of Wisconsin greenhouse were attacked and killed by a combination of a species of *Fusarium*, causing damping-off, and a powdery mildew, probably *Erysiphe polygoni* DC. Conidia of the powdery mildew were produced in abundance, but perithecia were not formed, perhaps because of the rapid death of the host seedlings.

Chimaphila umbellata frequently shows striking and very well-defined spots on the leaves. The spots bear globose fungal bodies, very likely immature perithecia of *Mycosphaerella*. So far, no mature Wisconsin specimen has come to my attention. Various other species of the Ericaceae are likewise very susceptible to spotting, but are similarly unproductive of identifiable parasites.

Galium boreale, collected at Tower Hill State Park, Iowa Co., May 18, bears a parasite which I am unable to classify as yet. The brown spotting of the affected areas of the host leaves is pronounced and conspicuous. In these areas are pycnidia which are short-rostrate and imperfectly developed below, amphigenous, but mostly epiphyllous, clustered in small groups on what might be considered an effuse stroma. They are about 100-150 μ diam. The conidia are cylindric, hyaline, markedly biguttulate, 10-17 x 3-4 μ. It seems possible that this might be regarded as a species of *Placosphaeria* and I am filing it under that genus for the present.

ALTERNARIA sp. has been found on small, sharply delimited spots on otherwise healthy leaves of young plants of *Acalypha virginica* at Arena, Iowa Co., July 17. I am of the opinion that this is a true parasite, but I am not sure of its proper systematic position. The spots are very noticeable, usually several per leaf, irregularly rounded, or sometimes elongate following the veins, occasionally confluent, dark brown with ashen centers, mostly 2-3 mm. diam. The conidiophores are epiphyllous, scattered or very loosely tufted, dark olivaceous, geniculate, several-septate, about 75-125 x 6-7 μ. The conidia are pale olivaceous, with 6-8 horizontal septa, about 125-150 x 12 μ, strongly attenuate in the upper half, with the attenuate portion forked occasionally. Not more

than two or three vertical septa have been observed in any of the conidia and some lack them entirely. These conidia are obviously of the non-catenate type and are very similar to those figured by Neergaard, in his monograph of the Danish species of *Alternaria*, for *Alternaria linicola* on *Linum* which is quite close to *Acalypha* systematically.

FUSARIUM sp. parasitized the leaves of several trees of *Tilia americana* at Ferry Bluff, Sauk Co., in the summer of 1948. Collections made in August did not show conidia, but those made in September had a profuse development. The conspicuous orbicular spots are about 1-3 cm. diam., once to several times zonate, grayish-brown, with darker narrow rings of zonation. The fruiting of the hyaline fungus is epiphyllous and tends to occur in concentric rings, following the zonation of the spots. Sections of young material show that the organism is fairly deep-seated in the host tissue, but is at the same time strongly erumpent. The subdisciform body of the sporodochium is almost pseudoparenchymatous, composed of closely compacted, gnarled hyphae. The sporodochia are roughly from 100-200 μ wide. Laxly flexuous appendages arise from the periphery of the disc and seem to have the function of anchorage to the substratum. These appendages, which show an occasional septum, may be twice as long as the disc is wide. The mature sporodochia are easily detached from the substratum, but there seems to be no doubt that they arise within it. In the mature fruiting bodies the appendages have largely disappeared and masses of the large, subfusoid, strongly curved macrospores are produced. They are up to 9-septate and, measured from tip to tip, without taking curvature into account, are from 50-80 x 5-7 μ. In mass the conidia appear grayish, but viewed individually they are hyaline.

ADDITIONAL HOSTS

The following hosts have not been previously recorded as bearing the fungi mentioned in Wisconsin.

SPHAEROTHECA HUMULI (DC.) Burr on *Gilia linearis*. Green Co., Belleville, July 24.

SPHAEROTHECA HUMULI var. FULIGINEA (Schl.) Salm. on *Erigeron annuus*. Sauk Co., Parfrey's Glen, August 12.

ERYSIPHE GRAMINIS DC. Conidia only on *Elymus villosus* (*E. striatus*). Green Co., New Glarus Woods, July 15.

ERYSIPHE GALEOPSIDIS DC. on *Physostegia parviflora*. Sauk Co., Cactus Bluff, Town of Prairie du Sac, August 20.

ERYSIPHE CICHORACEARUM DC. on *Parthenium integrifolium*. Dane Co., Madison, October 1. Also on *Silphium terebinthinaceum*. Same station and date.

CLAVICEPS PURPUREA (Fr.) Tul. Sclerotia on *Lolium perenne*. Dane Co., Madison, October 21, 1947. Coll. & det. J. G. Dickson.

PHYLLACHORA PUNCTA (Schw.) Orton on *Panicum boreale*. Dane Co., Madison, August 16.

USTILAGO STRIIFORMIS (West.) Niessl on *Poa compressa*. Waushara Co., Hancock, May 1947. Coll. & det. J. G. Dickson. Also on *Dactylis glomerata*. Walworth Co., Lake Geneva, May 23, 1947. Coll. & det. M. J. Thirumalachar.

COLEOSPORIUM SOLIDAGINIS (Schw.) Thum. II on *Aster shortii*. Green Co., New Glarus Woods, May 20.

PUCCINEA CORONATA Cda. II on *Lolium perenne*. Dane Co., Madison, October 21, 1947. Coll. & det. J. G. Dickson. Also II, III on *Hystrix patula* at Madison, August 23. Not listed in *Arthur's Manual* on the latter host.

PUCCINIA ELLISIANA Thum. I on *Viola cucullata*. Jefferson Co., Lake Mills, June 5. Closely associated with plants of *Viola pedatifida* bearing the same rust.

PUCCINIA EXTENSICOLA Plowr. I on *Aster shortii*. Green Co., New Glarus Woods, May 20. Apparently not hitherto reported on this host. Also on *Lactuca ludoviciana*. Dane Co., Madison, June 11. A scanty collection. Very common on *Lactuca canadensis* in Wisconsin.

PHOMA MARIAE G. W. Clint on *Lonicera tatarica*. Dane Co., Madison, April 24. The conidia in this specimen have a greenish tinge, and some of them show a median septum, formed, it appeared, just prior to germination. Also on *Lonicera dioica*. Vernon Co., Viroqua, November 3, 1947.

PIGGOTIA FRAXINI B. & C. on *Fraxinus pennsylvanica* var. *lanceolata*. Iowa Co., Arena, September 22, 1940. Wolf and Davidson (Mycologia 33: 538. 1941) state concerning this organism "The pathogen is polymorphic, possessing a conidial stage properly identified as *Marssonia fraxini* Ell. & Davis, a spermogonial and carpogonial stage, commonly designated *Piggotia Fraxini* Berk. & Curt., and a perithecial stage herein assigned to *Mycosphaerella effigurata* (Schw.) House."

PHYLLOSTICTA GUTTULATAE Halst. on *Oxalis violacea*. Dane Co., Madison, June 23. Davis reported *Phyllosticta oxalidis* Sacc. on *Oxalis stricta* from Wisconsin. In that species the conidia are described as 4 x 3 μ, but those in the two specimens collected by Davis are 6-10 μ long, and I find the same condition in specimens that I have taken. I suspect that *Phoma oxalidicola* Speg. is identical with *Ph. guttulatae*, and very likely also *Phyllosticta oxalidicola* P. Henn.

PHYLLOSTICTA VIOLAE Desm. on *Viola cucullata*. Jefferson Co., Lake Mills, June 30. Also at Madison, July 7.

PHYLLOSTICTA LIATRIDIS J. J. Davis on *Liatris squarrosa* var. *compacta* (smooth form). Dane Co., Madison, July 23. The pycnidia are larger than the 65 μ of the description, but the conidia are uniformly 10 x 4 μ as described.

PHYLLOSTICTA DECIDUA Ell. & Kell. on *Ratibida columnifera*. Jackson Co., Black River Falls, July 20, 1947. Coll. D. Grether. On this host the fungus has the aspect of a true parasite and there is no indication of any previous insect damage.

CONIOTHYRIUM FUCKELII Sacc. on *Rubus pubescens* (*triflorus*). Dane Co., Madison, August 9. On rounded grayish spots on the leaves, appearing parasitic. This fungus is the cause of a cane blight of cultivated raspberries, but there was no sign of infection on the weak, trailing stems of *R. pubescens*. The ascigerous stage is a *Leptosphaeria*.

ASCOCHYTA GRAMINICOLA Sacc. on *Hystrix patula*. Green Co., Brooklyn, June 21. Most of this material is on leaves which are also infected with *Scolecotrichum*.

ASCOCHYTA THASPII Ell. & Ev. on *Thaspium trifoliatum* var. *flavum* (*T. aureum*). Rock Co., Town of Magnolia, Sect. 7, June 21. On *Cicuta bulbifera*. Dane Co., Madison, August 26. Also on *Oxypolis rigidior* at Madison, July 19, and in Iowa Co., at Canyon Park near Dodgeville, August 18. On the latter host the infected areas are of large and indefinite extent.

STAGONOSPORA ALBESCENS J. J. Davis on *Carex lacustris*. Dane Co., Madison, July 30. Although the description indicates that this species produces definite spots, specimens in the herbarium, other than the type, do not show this, nor does the specimen on *C. lacustris*. In the field, infected plants of the latter host are most conspicuous, since the upper portions of the affected leaves have completely died back and are "lopped over" without exception.

STAGONOSPORA BAPTISIAE (Ell. & Ev.) Davis on *Baptisia leucophaea* (*bracteata*). Dane Co., Madison, July 1.

STAGONOSPORA ZONATA J. J. Davis on *Asclepias hirtella* (*Acerates floridana*). Dane Co., Madison, September 22.

SEPTORIA NODORUM Berk. on *Festuca obtusa*. Green Co., New Glarus Woods, June 21; Columbia Co., Poynette, July 10. Det. R. Sprague.

SEPTORIA STELLARIAE Rob. & Desm. on *Stellaria aquatica*. Lafayette Co., Red Rock, July 24.

SEPTORIA VIOLAE West. on *Viola incognita*. Iowa Co., Canyon Park near Dodgeville, August 18. An earlier collection by Davis on *Viola* sp. from Nekoosa, Wood Co., appears likewise to be on this host. The spots are large, brown, immarginate, with many pycnidia per spot.

SEPTORIA LITHOSPERMI Davis & Greene on *Onosmodium molle* var. *occidentale*. Green Co., Town of York, Sect. 3, July 24. Some of the conidia in this collection are as much as 100 μ.

SEPTORIA FUMOSA Peck on *Aster sagittifolius*. Racine Co., Racine, May 17, 1897. Coll. J. J. Davis. Davis tentatively referred this to *S. astericola* Ell. & Ev., but did not report it. It corresponds well with other specimens that have been filed under *S. fumosa*, although all of them have been on species of *Solidago*.

SEPTORIA HELIANTHI Ell. & Kell. on *Echinacea* (*Brauneria*) *pallida*. Green Co., Town of Mt. Pleasant, roadside prairie remnant, Sect. 35, August 7. In general, *Septoria helianthi*, when it develops on xerophytic hosts such as *Helianthus rigidus*, tends to have sporules which are somewhat more slender than those produced on a host like *Helianthus tuberosus*. *Echinacea pallida* is an outstanding xerophyte, in this case growing on a desiccated lime-capped hilltop, and the conidia are slender, many of them noticeably flexuous.

DILOPOSPORA ALOPECURI Fr. on *Festuca ovina*. Columbia Co., May 8. Coll. & det. M. J. Thirumalachar.

GLOEOSPORIUM CANADENSE Ell. & Ev. on *Quercus bicolor*. Iowa Co., Arena, June 9. *Gloeosporium bicolor* J. J. Davis seems to be distinct in its much greater spore size and entirely different type of lesion.

COLLETOTRICHUM GRAMINICOLUM (Ces.) Wils. on *Echinochloa pungens*. Sauk Co., Ferry Bluff, Town of Prairie du Sac, August 20. Also on *Bouteloua hirsuta*. Sauk Co., Cactus Bluff, Town of Prairie du Sac, September 18.

COLLETOTRICHUM PHOMOIDES (Sacc.) Chester on *Capsicum annuum*. Dane Co., Madison. Kendick and Walker (Phytopath. 38: 258. 1948) report natural infection of pepper fruits when the plants were in close proximity to infected tomato plants.

COLLETOTRICHUM SOLITARIUM Ell. & Barth. on *Aster linariifolius*. Dane Co., near Sauk City, August 12. Although this species seems not to have been reported on *Aster*, in view of the several parasites which go to both *Solidago* and *Aster*, it is not surprising that *C. solitarium* should do likewise. There is considerable variation in the size of the conidia, and in all of the numerous specimens on diverse hosts that I have examined many of the conidia are considerably longer and wider than the 12-14 x 2.5-3 μ of the description.

CYLINDROSPORIUM BETULAE J. J. Davis on *Betula lutea*. Iowa Co., Canyon Park near Dodgeville, August 18.

OVULARIA PULCHELLA (Ces.) Sacc. on *Agrostis alba*. Dane Co., Madison, August 7. Coll. & det. M. J. Thirumalachar.

OVULARIA HORDEI (Cav.) Sprague on *Glyceria grandis*. Dane Co., Madison, August 24.

CLADOSPORIUM EFFUSUM (Wint.) Demaree on *Carya ovata*. Sauk Co., Devils Lake, June 26, 1946.

HELMINTHOSPORIUM BROMI Died. (*Pyrenophora bromi*) on *Bromus tectorum*. Dane Co., Madison, June 23.

CERCOSPORELLA CANA Sacc. on *Erigeron glabellus*. Washburn Co., Trego, September 12, 1929. Coll. N. C. Fasset and W. T. McLaughlin. This is stunted and *Ramularia*-like, but seems best assigned here. The conidia are 22-33 x 3-3.5 μ, the conidiophores about 12-15 x 3.5 μ.

CERCOSPORA CARICINA Ell. & Dearn. on *Carex cristatella* (*C. cristata*). Lafayette Co., Red Rock, July 24.

CERCOSPORA ZEBRINA Pass. on *Trifolium procumbens*. Dane Co., Paoli, July 6.

CERCOSPORA VIOLAE Sacc. on *Viola pubescens*. Green Co., Albany, September 13.

CERCOSPORA ZIZIAE Ell. & Ev. on *Thaspium trifoliatum* var. *flavum* (*T. aureum*). Green Co., near Monticello, July 28.

CERCOSPORA RACEMOSA Ell. & Mart. on *Stachys palustris*. Dane Co., Madison, July 30.

CERCOSPORA UMBRATA Ell. & Holw. on *Bidens frondosa*. Dane Co., Madison, September 4. Also on *Biden cernua*, Madison, September 1, 1944. *Cercospora bidentis* Tharp is the species usually found on *B. cernua* in Wisconsin.

CERCOSPORA WISCONSINENSIS Chupp & Greene on *Prenanthes aspera*. Green Co., Albany, August 7.

ALTERNARIA SOLANI (E. & M.) Jones & Grout on *Lycopersicum esculentum*. Dane Co., Madison, September 7. Belatedly listed here for the sake of a record, since Davis seems not to have mentioned the fungus on this host in his notes.

LEPTOTHYRIUM PUNCTIFORME B. & C. on *Erigeron philadelphicus*. Bayfield Co., Drummond, June 24, 1930. Coll. N. C. Fassett. On a phanerogamic specimen in the University of Wisconsin Herbarium. Not reported on this host in Seymour.

TUBERCULINA PERSICINA (Ditm.) Sacc. on *Puccinia extensicola* Plowr. I on *Hieracium scabrum*. Dane Co., Madison, June 19. Also on *Puccinia minutissima* Arth. I on *Decodon verticillatus*, Madison, August 7.

ADDITIONAL SPECIES

The fungi mentioned have not been previously reported as occurring in Wisconsin.

SYNCEPHALIS species, parasitic on other Mucoraceae in Wisconsin, have been cultured and determined by C. W. Hesseltine as follows: *Syncephalis cornu* van Tiegh. & LeMonnier on *Rhizopus arrhizus* and on *Mucor* spp. *S. nodosa* van Tiegh. on *Mucor* spp. *S. depressa* van Tiegh. & LeMonnier on *Mucor* spp., and on *Pilobolus* sp. *S. tenuis* Thaxter on *Mucor* sp.

PERISPORIUM WRIGHTII B. & C. (*Stevensea* Trott.) on *Opuntia rafinesquii*. Sauk Co., Tower Rock near Denzer, March 20. Coll. R. I. Evans. This is the first mature Wisconsin specimen I have seen.

VENTURIA PALUSTRIS Sacc., Bomm. & Rouss. on *Potentilla palustris*. Dane Co., Madison, October 2. The perithecia are superficial, but confined to and epiphyllous on the dull purple, immarginate, rounded spots. It seems possible that this is connected with *Marsonia potentillae* (Desm.) Fisch., common on *Potentilla palustris*.

MYCOSPHAERELLA MELONIS (Pass.) Chiu & Walker on *Citrullus vulgaris* (watermelon). Sauk Co., Merrimac, August 27, 1947. Davis reported the imperfect stage of this fungus, on cucumber in Wisconsin, as *Ascochyta cucumis* Fautr. & Roum. Passerini in 1891 described the ascomycetous stage under the name *Didymella melonis* without understanding its connection with the *Ascochyta* stage.

Phaeosphaeria acori sp. nov.

Maculis conspicuis, pallido-brunneis vel cinereis, marginibus fusco-rufis vel purpureis, rotundatis vel elongatis, 1.5-10 mm., plerumque 2-3 mm., amphigenis; peritheciis nigris, subcuticulis, erumpentibus, gregariis, subglobosis vel planis aliquantum, ostiolatis, aparaphysatis, 100-150 μ diam.; ascis clavatis, crassis, octosporis, 60-70 x 13-15 μ; ascosporis olivaceis, triseptatis, fusoideis, rectis vel curvatis leviter, 25-35 x 4 μ.

Spot conspicuous, pale brown or cinereous with dark red or purplish borders, rounded or elongate, 1.5-10 mm., mostly 2-3 mm., amphigenous; perithecia black, subcuticular, erumpent, subglobose or somewhat flattened, ostiolate, aparaphysate, 100-150 μ diam.; asci stout-clavate, 8-spored, 60-70 x 13-15 μ; ascospores olivaceous, triseptate, fusoid, straight or slightly curved, 25-35 x 4 μ.

On living leaves of *Acorus calamus*. Madison, Dane County, Wisconsin, U. S. A., August 24, 1948.

This is evidently fairly similar to *Leptosphaeria microscopica* var. *calami* Karst., except that in that species the ascospores were 20-24 x 6 μ, and it occurred on decaying leaves. In connection with the account of *L. microscopica* var. *calami* (Hedwigia 22: 179. 1883) there is mention of an ad interim species, *Leptosphaeria acori*, not formally described so far as I can learn. This diverges even more widely from the Wisconsin material.

PSEUDOPLEA TRIFOLII (Rostr.) Petr. on *Trifolium repens* (Ladino). Waushara Co., Hancock, November 7, 1947. Coll. & det. J. G. Dickson.

PHYLLOSTICTA TOXICA Ell. & Mart. on *Rhus radicans*. Columbia Co., Black Hawk's Lookout near Prairie du Sac, August 20.

SPORONEMA CAMELLIAE Earle on *Camellia japonica*. On a plant in a greenhouse at Madison. Coll. J. W. Thomson, December 1947.

ZYTHIA AURANTIACA (Peck) Sacc. on *Cornus alternifolia*. Green Co., Oakly, May 1. This appears to be an active parasite on the twigs and branches, causing them to die back.

Phomopsis liatridis sp. nov.

Maculis rotundatis, 3-5 mm. diam., centris pallido-brunneis, marginibus latis, purpureis; pycnidiis nigris, gregariis vel confertis, subglobosis vel applanatis, plerumque epiphyllis, 175-275 μ diam.; *Phoma*-conidiis hyalinis, subfusoideis, plerumque biguttulatis, 12-17 x 4-7 μ; scolecosporis hyalinis, continuis, plerumque curvatis fortiter, 15-30 x 1.5 μ.

Spots rounded, 3-5 mm. diam., center pale brown, border wide, purplish; pycnidia black, gregarious or crowded, subglobose or flattened, mostly epiphyllous, 175-275 μ diam.; *Phoma*-type conidia hyaline, subfusoid, mostly biguttulate, 12-17 x 4-7 μ; scolecospores hyaline, continuous, mostly strongly curved, 15-30 x 1.5 μ.

On living leaves of *Liatris ligulistylis*. Madison, Dane County, Wisconsin, U. S. A., August 9, 1948.

An occasional spot bears a single very large pycnidium, up to 350 μ, or even more. It appears that these are formed by the coalescence of two or more smaller pycnidia, although this would be difficult to demonstrate. On some lesions the pycnidia are so crowded as to be angled by mutual pressure, and indeed their contiguous walls appear to be fused in such cases. Several of the affected leaves have quite elongate lesions on the midribs. Most of the amerospores are rather sharply pointed at the apices. The scolecospores are frequently more strongly tapered at one end than at the other. Their width is constant, whatever their length.

Coniothyrium pallidospermum sp. nov.

Maculis pallido-brunneis, marginibus angustis rufis, rotundatis vel subfusoideis interdum, 2-5 mm. diam., plerumque 3-4 mm.; pycnidiis sparsis vel gregariis, epiphyllis ferme, amphigenis interdum, globosis vel subglobosis, fuligineo-brunneis, ostiolatis, 100-150 μ diam.; conidiis brevibus, cylindraceis vel ellipsoideis late, vel interdum ovatis, pallido-fuligineis, muris tenuibus, 4-7 x 3-4 μ.

Spots pale brown with narrow reddish border, rounded or sometimes subfusoid, 2-5 mm. diam., mostly 3-4 mm.; pycnidia scattered or gregarious, usually epiphyllous, occasionally amphigenous, globose or subglobose, sooty

brown, ostiolate, 100-150 μ diam.; conidia short cylindric or broadly ellipsoid, occasionally ovate, pallid, fuligenous, thin-walled, 4-7 x 3-4 μ.

On living leaves of *Carya cordiformis*. New Glarus Woods Roadside Park, one mile south of New Glarus, Green County, Wisconsin, U. S. A., August 5, 1948.

Organisms with conidia as pale as these have sometimes been placed in *Phyllosticta*, but in my opinion would be better assigned to *Coniothyrium*. When a pycnidium is mounted in water the cirrhus of ejected conidia appears black under low magnification.

I am well aware of the manifold fungi which can be found on sharply defined spots on the leaves of hickory, particularly *Carya ovata*, and it seems likely that many of these have developed saprophytically. In this instance, however, trees scattered over a number of acres consistently bore only the one type of spot, and with equal consistency the pycnidia on the spots proved all to belong to the same organism.

ASCOCHYTA ARMORACIAE Fckl. on siliques and leaves of *Brassica juncea*. Iowa Co., Canyon Park near Dodgeville, August 18. Doubtfully parasitic. Although pycnidia occur on still green pods and leaves there is evidence of preceding insect attack. The Wisconsin material corresponds closely to No. 839 of Jaap's Fungi Selecti Exsiccati, issued as this species, on *Armoracia rusticana*. Many of the conidia lack a median septum.

ASCOCHYTA VALERIANAE Smith & Ramsb. on *Valeriana officinalis*. Dane Co., Madison, July 7. Correspondence with the description is close, except that the pycnidia are amphigenous instead of epiphyllous, and are mostly somewhat smaller than 120-180 μ as described. In any one pycnidium probably 80 per cent or more of the conidia are immature and lack the septum.

Ascochyta rudbeckae (Ell. & Ev.) n. comb. Ellis and Everhart based *Phyllosticta rudbeckiae* on a specimen on *Rudbeckia laciniata* from Kenosha Co., Wis., collected Sept. 23, 1894 by J. J. Davis (Proc. Acad. Nat. Sci. Phila. 47: 430. 1895). Examination of a number of collections made by Davis and myself demonstrates that when mature this species is an *Ascochyta*. The lesions are of the rather large, opaque-blackish, effuse type that are commonly characteristic of *Ascochyta*, but not of *Phyllosticta*.

STAGONOSPORA FOLIICOLA (Bres.) Bubak on *Phalaris arundinacea*. Dane Co., Madison, August 23. Earlier collections have been variously referred to *Stagonospora intermixta* (Cke.) Sacc. and *Stagonospora arenaria* Sacc. Sprague (Mycologia 40: 306. 1948) states that specimens determined by him as *S. arenaria* have proved to be immature *S. foliicola*. A comparison of the 1948 Wisconsin specimen with European material of *S. foliicola* certainly shows great similarity.

Stagonospora canadensis sp. nov.

Maculis variis, orbiculatis vel angulatis, plerumque 3-5 mm. latis, saepe confluentibus, fusco-brunneis, marginibus inconspicuis, elevatis leviter; pycnidiis

epiphyllis, sparsis vel gregariis, paucis, 125-175 μ diam., subglobosis, nigro-brunneis, pseudoparenchymaticis, ostiolis parvis; conidiophoris brevibus, fere obsoletis; conidiis hyalinis, oblongatis, 7-9 x 20-28 μ, 1-2-septatis, raro 3-septatis.

Spots variable, orbicular or angled, mostly 3-5 mm. wide, often confluent, dark brown, margins inconspicuous, slightly raised; pycnidia epiphyllous, scattered or gregarious, few, 125-175 μ diam., subglobose, blackish-brown, pseudoparenchymatous, ostioles small; conidiophores very short, almost obsolete; conidia hyaline, oblong, 7-9 x 20-28 μ, 1-2-septate, rarely 3-septate.

On living leaves of *Anemone canadensis*. Arena, Iowa County, Wisconsin, U. S. A., May 18, 1948. Collected also at Verona, Dane Co., and near Lake Mills, Jefferson Co.

Stagonospora anemones Pat. is mentioned by Davis as of questionable occurrence on leaves of *Anemone canadensis* in Wisconsin (Trans. Wis. Acad. Sci. 24: 289. 1929). Davis stated "While examining leaves of *Anemone canadensis* for the presence of oospores of *Plasmopara pygmaea* it was found that in addition to the oospores there were present pycnidia about 100 μ in diameter containing hyaline oblong conidia 18-30 x 3-7 μ, 1-2 septate. Whether or not this is *Stagonospora anemones* Pat. I do not know." This latter species is described as having pycnidia 500-1000 μ diam. and 3-septate conidia 26-30 x 3-4 μ. It occurred on the petioles of dead plants of *Anemone* sp. in Yunnan, China. It seems highly improbable to me that these can be the same. Davis did not put a specimen in the Wisconsin Herbarium, although in his *Parasitic Fungi of Wisconsin* he lists *S. anemones* Pat. as occurring in the state.

Stagonospora canadensis is one of those species which are on the borderline between *Ascochyta* and *Stagonospora*. In my specimens the 1-septate conidia are more numerous than the 2-septate, but there are many of the latter and the septations are sharply defined.

SEPTORIA ELYMI f. ELYMINA (J. J. Davis) R. Sprague on *Agropyron smithii*. Green Co., Monticello, June 13. Det. R. Sprague. This is a new combination made by Sprague (Mycologia 40: 302. 1948) for the form of *Septoria elymi* Ell. & Ev. which Davis described, from Wisconsin material on *Elymus virginicus*, as *Septoria bromi* var. *elymina*.

SEPTORIA PUNCTOIDEA Karst. on *Carex convoluta* Mack. Dane Co., near Sauk City, May 7. The pycnidia are very small, not over 65 μ diam., and some only 40 μ. Each developed substomatally. The conidia are 12-22 x 1.5 μ. The distal portions of the leaves have died back and most of the pycnidia occur at the base of the dead portion. This is one of group of organisms causing die-back of leaves in *Carex*, but seems distinct in the small pycnidia.

Septoria violacea sp. nov.

Maculis cinereis cum marginibus luteis, in foliis marginibus, formis et

amplitudinibus variis; pycnidiis gregariis, epiphyllis, pallido-brunneis, subglobosis, infra imperfectis, subrostratis, ostiolis cellis fuscis conseptis, 50-100 μ diam., plerumque ca. 80 μ; conidiis hyalinis, subfusoideis, curvatis diversis, interdum laxis, 35-55 x 2.5-3.5 μ, plerumque 6-8-septatis.

Spots cinereous with orange border, marginal, size and shape variable; pycnidia gregarious, epiphyllous, pale brown, subglobose, tending to be imperfectly developed below, subrostrate, ostiole surrounded by a raised ring of dark cells, 50-100 μ diam., mostly about 80 μ; conidia hyaline, subfusoid, variously curved, sometimes laxly so, 35-55 x 2.5-3.5 μ, mostly 6-8-septate.

On living leaves of *Oxalis violacea*. Madison, Dane County, Wisconsin, U. S. A., June 23, 1948.

With suitable magnification the pycnidia are quite noticeable because of the prominently developed dark ring about the ostiole. The conidia are yellowish in mass, but hyaline viewed individually. They are obtuse at one end. None are straight, but the degree and type of curvature is quite variable. The dimensions of the conidia are much greater than those of *Septoria oxalidis* Lind. and *S. acetosella* Dearn. & House, which are perhaps conspecific. *S. violacea* is possibly allied to *Stagonospora hygrophila* Sacc., which occurred on *Oxalis acetosella*.

SEPTORIA GUARINA Ell. & Kell. on *Guara biennis*. Dane Co., Mazomanie, August 20. Many of the conidia are about 100 μ long. Very close to *Cylindrosporium*.

Septoria cornicola Desm. var. **ampla** var. nov.

Sporulis ca. 25-40 x 3.5-5 μ, rectis vel subflexuosis.

On living leaves of *Cornus racemosa* (*C. paniculata*). Madison, Dane County, Wisconsin, U. S. A., September 16, 1948.

I have encountered this on several occasions in different years. In my experience it is a late season manifestation and occurs on leaves which are on the verge of senescence. As would be expected, bridging forms between this and the typically narrower, often curved sporules of *S. cornicola* can be found. Many of the conidia are only indistinctly septate. The lesions frequently are encircled by a band of yellowed tissue.

SEPTORIA DIGITALIS Pass. on *Besseya* (*Synthyris*) *bullii*. Green Co., Albany, May 1. The pycnidia are rather closely clustered on sordid spots on the persistent green leaves of the basal rosette. The continuous conidia are 20-30 x 1.5 μ and were being extruded in cirrhi. As described, the narrow range of 25-30 x 1.5 μ is given.

SEPTORIA VIBURNI West on *Viburnum opulus* (cult.). Dane Co., Madison, July 30. The European host has been growing in a nursery in the University of Wisconsin Arboretum for a number of years, but this is the first

time I have noticed this fungus. The semi-emergent pycnidia and vacuolate conidia seem characteristic.

SEPTORIA CREPIDIS Vestergr. on *Crepis tectorum*. Douglas Co., Solon Springs, June 13, 1942. Coll. J. W. Thomson. On leaves of a phanerogamic specimen in the University of Wisconsin Herbarium.

Septoria socia Pass. on *Chrysanthemum balsamita* var. *tanacetoides*. Dane Co., Madison, August 13. The fungus is on large dead areas on the leaves. The conidia are about 25 x 1.5 μ. This specimen corresponds well with Krieger's Fungi saxonici No. 1392 on *Chrysanthemum leucanthemum*.

Hendersonia spartinae sp. nov.

Maculis elongatis, pallido-brunneis vel albidis, marginibus brunneis distinctis, interdum confluentibus, 5-12 x 2-3 mm.; pycnidiis epiphyllis, sparsis vel gregariis, nonnihil applanatis, late ellipsoideis vel subcirculis, olivaceis, ca. 180-200 x 200-250 μ; conidiis pallido-olivaceis, distincte 3-7-septatis, plerumque 5-septatis, apicibus obtusatis, medietatibus leviter latioribus, 25-35 x 6-8 μ.

Spots elongate, pale brown or whitish with distinct brown border, sometimes confluent, 5-12 x 2-3 mm.; pycnidia epiphyllous, scattered or gregarious, somewhat flattened, broadly ellipsoid or subcircular in outline, olivaceous, approx. 180-200 x 200-250 μ; conidia pale olivaecous, distinctly 3-7-septate, mostly 5-septate, obtuse at both ends, slightly wider in the middle, 25-35 x 6-8 μ.

On living leaves of *Spartina pectinata*. Madison, Dane County, Wisconsin, U. S. A., July 26, 1948.

The lesions are sharply delimited, and the fungus appears to be truly parasitic. Relatively few species of *Hendersonia* have been reported on Gramineae in North America. This somewhat resembles *Hendersonia agropyri* Rostr., but differs in the greater number of septa in the spores.

COLLETOTRICHUM OMNIVORUM Halst. on *Hosta plantaginea*. Dane Co., Madison, September 4. The infection picture is not complicated by the presence of other fungi, so it is probable that the organism developed parasitically.

RAMULARIA PASTINACAE (Karst.) Lindr. Vestergr. on *Pastinaca sativa*. Dane Co., Madison. Kendrick and Walker (Phytopath. 38: 258. 1948) reunder *Cercospora pastinacae* (Sacc.) Pk. leads to the conclusion that there is an intergrading series of forms on this host, running from *Cercospora* to *Cercosporella-Ramularia*. This specimen is at the hyaline extreme and seems best set apart. Savile (Canadian Plant Dis. Surv., 23rd Ann. Rep.: 54. 1943) discusses this perplexing series and the associated nomenclatorial problems. He considers *Cercospora pastinacae* as distinct, but I doubt that this is so.

THALLOSPORA ASPERA L. S. Olive (new genus) is described (Mycologia 40: 11. 1948) as a systemic and obligate parasite of *Veronica peregrina* in Louisiana. As Olive states, I mentioned that this occurs on *V. peregrina* in Wisconsin (Trans. Wis. Acad. Sci. 35: 121. 1944). As a matter of fact the

late J. J. Davis had been familiar with this organism for many years and first pointed it out to me in 1935, when we collected it at Muscoda in Grant Co. I have since found it at Madison. I was unable to detect mycelium in the host, except in the ovaries, but Olive states that hyphae penetrate throughout most of the host plant. He considers that the rough, branched structures which pack the host fruits are conidia (thallospores) formed by hyphal fragmentation. Like myself, Olive was unable to culture the fungus.

HELMINTHOSPORIUM MONOCERAS Drechsler on *Echinochloa pungens*. Sauk Co., Ferry Bluff, Town of Prairie du Sac, August 20. Most of the conidia in this specimen are widest somewhat below the middle, and nearly all approach, or even slightly exceed, the described upper limit of 22 μ. This is nevertheless a striking and characteristic species. On this host there is no definite spotting and the infection is in the midrib region.

CERCOSPORELLA INCONSPICUA (Wint.) v. Hoehn. on *Lilium michiganense*. Jefferson Co., Faville Prairie near Lake Mills, June 5. I suspect that *C. veratri* Peck and *C. subterminalis* Peck, and perhaps other Cersosporellae on Liliaceae, are identical with this species, originally reported on *Lilium martagon* from Central Europe. The name is not particularly apt, for the lesions are large and very noticeable. This parasite is evidently highly destructive, for a number of small plants and seedlings were brown and dead following attack

CERCOSPORELLA BRASSICAE (Faut. & Roum.) v. Hoehn. on *Brassica juncea*. Iowa Co., Canyon Park near Dodgeville, August 18. Doubtfully parasitic on the siliques. Det. Chas. Chupp. Specimens on leaves of other species of *Brassica* appear parasitic.

Cercospora salicis Chupp & Greene sp. nov.

Maculis numerosis, parvulis, angulosis vel rotundatis vel irregularibus, rufo-brunneis fuscis, 0.5-2 mm., diam., vel confluentibus interdum; fasciis epiphyllis plerumque; stromatibus nullis vel cellis paucis; fasciis densis, compactis vel divergentibus; conidiophoris aequalibus olivaceo-brunneis palladis, latis irregularibus vel tenuatim supra leviter, rectis vel flexis, septatis restricte, non ramosis vel ramis rudibus prope apicibus obtusis, 0-1-geniculatis, 3.5-5 x 15-45 μ; conidiis pallido-olivaceis, cylindraceis vel cylindraceo-obclavatis, rectis vel curvis leviter, 1-7-septatis, basibus subtruncatis, apicibus obtusis, 2-4.5 x 20-70 μ.

Spots numerous, minute, angular, rounded or irregular, dark reddish-brown, 0.5-2 mm. diam., or sometimes confluent; fruiting mostly epiphyllous; stromata none or only a few cells; fascicles dense, compact to divergent; conidiophores uniform pale olivaceous brown, irregular in width or slightly attenuate upward, straight or bent, sparingly septate, not branched, or with incipient branches near the blunt tips, 0-1-geniculate, 3.5-5 x 15-45 μ; conidia pale olivaceous, cylindric, or the longest cylindro-obclavate, straight to slightly curved, 1-7-septate, base subtruncate, tip obtuse, 2-4.5 x 20-70 μ.

On living leaves of *Salix alba*. Madison, Dane County, Wisconsin, U. S. A., September 28, 1948. Coll. H. C. Greene.

The olivaceous tufts are mostly confined in a compact mass to the centers of the spots. When the conidia are persistent the phores, at first glance, may appear much longer than indicated in the description. Sizeable areas may be produced by coalescence of the small spots.

CERCOSPORA PETUNIAE (Saito) Muller & Chupp on *Petunia hybrida*. Dane Co., Madison, September 11. Det. Chas. Chupp.

FUSARIUM SARCOCHROUM (Desm.) Sacc. on *Acer negundo*. Dane Co., Madison, August 31. Perhaps doubtfully parasitic. However, the fungus occurred on a very distinct lesion on a living green twig, and there was no indication that any other agent was primarily responsible for the necrosis.

The Ovule and the Development of the Female Gametophyte in Homonia retusa Muell, and Euphorbia oreophila Miquel

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The Euphorbiaceae have been chosen by many investigators for embryological studies because of the extreme variability occurring in the family. The review of the types of development of the female gametophyte (Maheswari, 1942) stresses the necessity of the revision of embryological studies in the family. For example, on reinvestigation, *Euphorbia heterophylla* was shown to conform to the monosporic eight-nucleate type of embryo-sac (Maheswari, 1942) and not to the *Adoxa* type as was reported (Sanchez, 1938). A brief account of the development of the female gametophytes of *H. retusa* Muell, and *E. oreophilla* Miquel, is presented here.

Materials and Methods

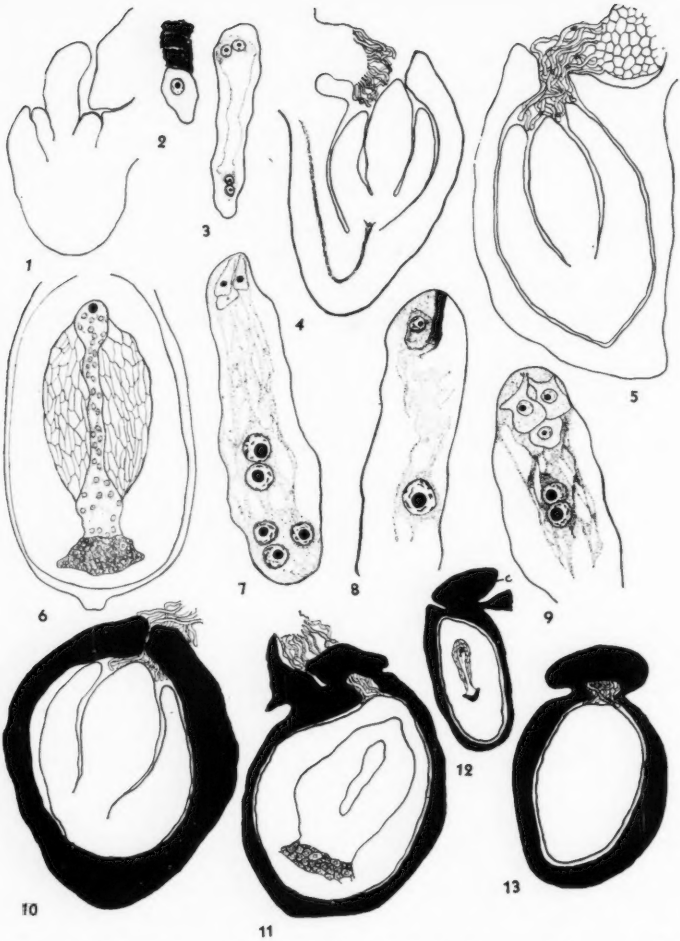
Homonia retusa Muell (Syn. *Adelia retusa*)is a small rigid glabrous shrub with stout woody branches, growing wild on river banks. The material was collected during the monsoon season at Thirthahalli, Mysore, India on the beds of the river Tunga. *Euphorbia oreophylla* Miquel is a perennial erect herb distributed throughout the malnad tracts. The material was collected in late March 1946 at Mercara, Coorg, India.

The materials were fixed at intervals of time between 9 a.m. and 3 p.m., in formalin-acetic-alcohol and, after the usual dehydration and infiltration methods, were imbedded in paraffin. Sections were cut 10 μ to 18 μ thick, stained according to Heidenhein's iron hematoxylin schedule and destained in a saturated solution of picric acid. Eosin in clove oil was used as a counterstain.

Observations

The ovule.—The ovules are anatropous and have two unfused integuments. The outer integument is 7 to 8 cells thick through most of its length but at the micropylar region it is 15 to 20 cells thick. The short micropyle is constituted mostly by the outer integument. The inner epidermis of the inner integument of *H. retusa* contains tannin, a conspicuous feature at all stages of development (figs. 14, 15). The nucellus is massive in both the species and in *E. oreophylla* it extends beyond the integuments early in ontogeny.

A well-developed conducting strand connecting the main vascular system in



Figs. 1-13.—*Euphorbia oreophila* Miquel.—1. Early development of the ovule. The nucellus is profuse and outgrows the integument (×528); 2. Linear tetrad (×1900); 3. Four nucleate sac (×1900); 4. Development of the hairy obdurator (×132); 5. Showing hairs in the micropyle arching over the nucellus, the outer integument remaining free from the inner (×132); 6. Post fertilization stage. The embryo-sac has formed a tube and has come in contact with the pad of tissue at the chalazal region. The nucellus forms a thin jacket (×120); 7. The eight-nucleate sac. The antipodals have organized into cells prior to the organization of the egg apparatus in the fusion of the polars (×1900); 8. Fertilization (×950); 9. Showing the hooked synergids and the late fusion of the polars (×800); 10-13. Showing the development of the caruncle. The outer integument is shaded dark. Note the hairs of the obdurator which are crushed by the growth of the caruncle. In fig. 12 caruncle is marked C. (Figs. 10, 11, 13 ×132; 12 not in scale.)

the placenta is evident from the inception of the ovule in *H. retusa*. It extends through the funiculus and spreads at the chalazal region of the ovule. As the ovule matures the procambial strands differentiate and branch profusely at the chalazal region forming a pad of vascular tissue (fig. 14).

In *E. oreophylla* slender thread-like processes, each with a prominent nucleus, are developed from the placenta just beneath the stylar canal (fig. 4). These together with the basal portion form the obdurator. The presence of the obdurator is described for some of the other members of the Euphorbiaceae such as *E. hirta, E. prolifera, E. wallichii* (Kajale & Rao, 1943), and *E. thymiflora* (Banerji & Dutt, 1944). The obdurator arches over the micropyle and penetrates it where the hairs cover the nucellus (fig. 5). The obdurator and its development is described in several families of angiosperms. In the Araliaceae (Ducamp, 1902; Pigott, 1914; Gopinath, 1944), Labiatae (Bushnell, 1936; Murthi, 1940), Rosaceae and Umbelliferae, its origin is reported to be from the funiculus (Schnarf, 1931). In Thymeliaceae and Plumbaginaceae (Dahlgreen, 1916) it arises from the base of the stylar canal. In the Euphorbiaceae so far investigated, the obdurator originates from the placenta and may grow into a pad of tissue or hairlike growths. In either case it grows across the opening of the micropyle. Various functions are attributed to the obdurator in the other families, such as the conduction of the pollen tube, etc. The exact significance of its presence and entry into the micropyle in *E. oreophylla* cannot be definitely stated. Banerji and Dutt (1944) are of the opinion that the massive obdurator in *Putranjiva Roxburghii* and *Trewia nudiflora* "comes to lie just above the micropyle, so that the pollen tube has to follow a circuitous route to reach the embryo-sac." In some species of the Araliaceae (Gopinath, 1944) it is considered to have a chemotactic influence guiding the pollen tube into the micropyle. It is possible that in *E. oreophylla* they secrete chemotropic substances orientating the pollen tube. The fact that the pollen tube grows through the obdurator into the micropyle and embryo-sac supports this inference. The obdurator remains a conspicuous feature of the ovule of *E. oreophylla* until fertilization.

Development of the embryo-sac.—The archesporium is hypodermal in both species and cuts off a parietal and a megaspore mother cell. The latter after undergoing the usual meiotic divisions, forms a linear tetrad of megaspores of which the chalazal one enlarges and gives rise to the eight-nucleate embryo-sac, derived according to the monosporic eight-nucleate type (figs. 2, 3, 8, 10, 16-18). The organization of the egg apparatus, the polar nuclei and the antipodals proceeds in the usual manner. In *E. oreophylla* a few sacs show an early organization of the antipodal cells (fig. 7); in *H. retusa*, the antipodals are nuclear. In both species the antipodals degenerate just prior to fertilization. The polar nuclei are in the middle of the embryo-sac. The synergids initially pear-shaped, later develop prominent hooks (figs. 9, 19). In both species the synergids are devoid of vacuoles. The egg lies close to the synergids. In the mature embryo-sac of *E. oreophylla* the cytoplasm is very dense.

Fertilization is porogamous. The synergids disorganize after the entry of

the pollen tube (fig. 8). Syngamy and secondary fertilization are simultaneous.

Post- fertilization changes in the ovule are interesting in *E. oreophylla*. Some of the chalazal cells become rich in cytoplasm and take a deep stain. As development proceeds these cells become more and more conspicuous and form a pad of tissue analagous to the hypostase. The chalazal end of the embryo-sac elongates and extends through the nucellus and comes in contact with this conspicuous pad of tissue. The embryo-sac after reaching this tissue, spreads laterally. Whether this pad of tissue is of a nutritional nature or whether it arrests the further growth of the embryo-sac is a matter of dispute (figs. 6, 12). The endosperm is characteristically of a free nuclear type (figs. 6, 20). The free endosperm nuclei migrate and are found distributed throughout the embryo-sac (fig. 6). Wall formation occurs later when the nucellus becomes thin and constitutes a jacket of loose thin-walled cells around the embryo-sac.

The development and morphology of the caruncle.—Though the presence of a caruncle is a characteristic feature of some genera of the Euphorbiaceae, very little attention has been paid to an understanding of their development and morphology. In other families where its presence is reported, its origin is attributed to the funiculus or the obdurator (Araliaceae: Pigott, 1944; Gopinath, 1944). Rendle (1925) says that in Euphorbiaceae "the ovules are generally provided with a caruncle or an obdurator which persists in the seed. It is an outgrowth from the placenta at the base of the funicle which covers the micropyle like a lid or hood and plays an important part in the conduction of the pollen tube." In *E. oreophila* the development of the caruncle has been studied in detail. Figures 10-13 represent the various stages in the development of the caruncle. During the post-fertilization stages the outer integument enlarges at the micropylar region (fig. 11). The cells rapidly increase in number and size and the micropyle constituted by the outer integument, is virtually closed. The hairs of the obdurator are clearly seen in the cavity above the nucellus (fig. 13). As growth continues, the outer portion of the outer integument fuses completely and grows distally with the result that the caruncle is formed (figs. 12, 13). It is evident that the formation of the caruncle is due entirely to the growth of the integument and not to the funiculus or any portion of the obdurator. The inner integument grows enormously thick and coalesces with the outer.

The details of the embryo development could not be traced in either of the species studied. Only the later stages as illustrated show an irregular mass of cells devoid of a suspensor.

SUMMARY

Development of the female gametophyte in *Homonia retusa* Muell, and *Euphorbia oreophila* Miquel, is reported.

The ovule is bitegumentary and the outer integument remains free from the inner until the eight-nucleate stage of the embryo-sac development. The

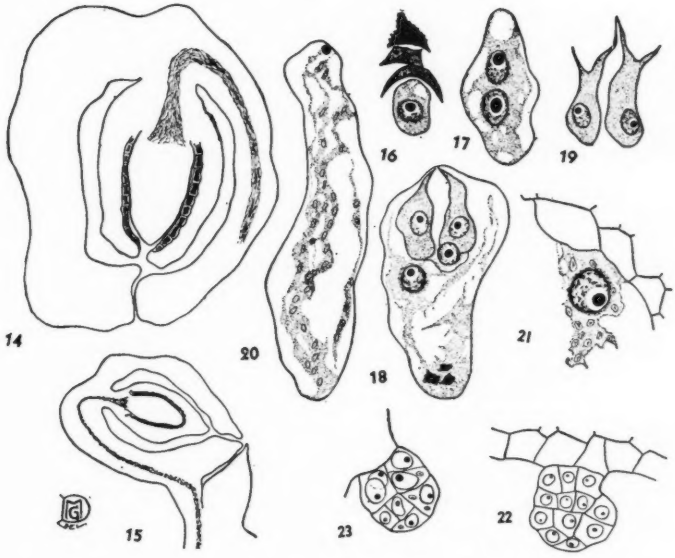
micropyle is constituted chiefly by the outer integument. The nucellus is massive and before archesporial development, has grown beyond the integument. An obdurator in *E. oreophila* is described.

The development of the embryo-sac is of the monosporic eight-nucleate type. Fertilization is porogamous.

The caruncle which is manifest in mature seed of *E. oreophila*, is a product of the outer integument.

In *E. oreophila* the embryo-sac shows polarities in growth in the post-fertilization stages.

The embryo is formed by the irregular divisions of the zygote and both the basal and terminal cells take part in the formation of the embryo.



Figs. 14-23. *Homonia retusa* Muell.—14. Development of the integuments, the conducting strand, and the deposition of tanin in the inner epidermis of the inner integument (not drawn to scale); 15. The anatropus ovule to show the funiculus and the micropyle formed mainly by the outer integument (×200); 16. Linear Tetrad. Chalazal megaspore enlarging (×1900); 17. Two nucleate embryo-sac before vacuolation (×1900); 18. Embryo-sac. Note the synergids, the secondary nucleus and the degenerated antipodals (×1900); 19. Synergids at a later stage, developing prominent hooks. The absence of vacuole in the synergids has to be noted (×1900); 20. The free nuclear endosperm and the embryo which appears insignificant (×1900); 21. The zygote with starch grains surrounding it (×1900); 22, 23. Stages in the embryo development (×1900).

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Book Reviews

ANIMAL COLOUR CHANGES AND THEIR NEUROHUMOURS. By George Howard Parker. Cambridge University Press, The Macmillan Co., N. Y. 1948. x+377 pp., 126 figs. $6.50.

Subtitled, *A Survey of Investigations, 1910 to 1943*, this book is all of that and more. It is difficult to conceive how a more complete or more readable summation of progress in the field of pigmentary effector systems during these years could be achieved. It can well stand as a model for future surveys of a like nature. Perhaps no biologist writing today is better qualified to undertake a work of this kind than Parker, for most of the research chronicled in these pages was either done or begun in the Harvard Laboratories under his guidance and inspiration. A large measure of it is the result of his own investigations, accomplished after he had retired from active teaching. All of it is an integrative work of the first order and defines the borders of our knowledge with such clearness and precision that no reader can long remain in ignorance of where they are. Like all good scientific literature, it raises more questions than it answers.

The organization of the book is logical and effective. The pigmentary responses of the various animal groups are first surveyed in phylogenetic order. Each section includes a complete and detailed account of the type of chromatophores seen, the mechanisms operating to produce changes in the distribution of their pigment and, where pertinent, a discussion of how these are influenced by environmental factors. This material roughly comprises about two-thirds of the book. Next follows a series of chapters covering various special aspects of chromatophore function, including a discussion of their growth and development, their genetics, their responses to various environmental stimuli (such as light, heat, pressure, etc.), and a consideration of such matters as chromatophore pulsations and the ecology of color changes. In this last chapter Parker sums up the various attempts biologists have made to explain the significance of color changes. It will come as no surprise that most men have emphasized their adaptive value, for purposes of protection, aggression or mating. Others, however, have recognized that they may serve as radiation screens, as aids in temperature regulation, or even may function in an excretory capacity. There is little experimental evidence to support any of these views, except possibly protective coloration, and it is astounding that the purpose of such a widespread phenomenon should still be a matter of general disagreement. It is almost as if science were still puzzled about the significance of the circulation. It is very doubtful if nature designed pigment cells purely for their decorative value, or to serve as objects of the biologist's curiosity. In all probability chromatophores have no single function but serve different animals in different ways. Here in itself is a research field that might be readily expanded. For instance, it should not prove too difficult to decide whether in the reptiles, and possibly in the amphibians as well, shifts in the distribution of pigment may not aid in regulating body temperature. Sumner's pioneer work on the protective value of color changes could well be explored further. The original function of the chromatophore will probably forever elude us for, whatever it was, it has probably long since been disguised by secondary adaptations.

The bibliography at the end of the book is probably as complete as human industry can make it. It includes all titles bearing on chromatophores published between 1910 and 1943 and will be of inestimable value to the student. Enough overlap has been allowed with Fuch's monumental review (which appeared in 1914) to guarantee continuity back to the days of Aristotle. Unfortunately the index is not up to the standard set by the rest of the book. More completeness and more detail at this point would add greatly to the usefulness of the book.

Parker shows with great clarity how a multiplicity of controlling systems are built up from the three basic and fundamental types of chromatophore responses. These may be classified as (1) direct responses to stimuli such as light and heat, (2) responses to

nervous stimulation, and (3) responses to hormonal stimulation. Using these three types a seemingly endless number of permutations can be constructed. It seems not unlikely that in primitive animals direct responses were the rule and that the same still holds true during the early embryonic life of modern vertebrates. However, as development proceeds the chromatophores ultimately come to be completely governed in their activities by either nerves or hormones, and are integrated into the body's economy just as are the muscles and the glands. In the cephalopods, for example, all control resides in the nervous system, while in the crustaceans direction is completely in the hands of one or more hormones. In the vertebrates, however, the controlling mechanisms are mixed in a most bewildering fashion. In the fishes, the balance is even between nervous and hormonal factors, but in the amphibians nervous control had been secondarily discarded in favor of hormones. On the other hand, the reptiles subordinate the influence of hormones and concentrate on the influence of the nervous system.

It is among fishes that the most varied responses are seen, and it is to an understanding of the forces operating within this group that Parker directed most of his attention during the recent years. Among other things, his concept of neurohumoral control grew out of this work. It has always seemed to this reviewer that Parker's contribution to our understanding of how the nerve impulse is transmitted across the myoneural junction has never been adequately recognized or appreciated. It is not our purpose to argue the merits or demerits of the various aspects of this theory, but it should be emphasized here that Parker was among the earliest to recognize this problem and to approach it experimentally. It is true that his interpretations have been largely ignored and the reader not fully informed in these matters should be warned that Parker's views would be considered unacceptable by many of his contemporaries. This, however, does not necessarily mitigate against their soundness or their usefulness.

One cannot but be impressed by the classic simplicity of Parker's experiments. The manner of their execution stands in sharp contrast to the bewildering array of electronic or photoelectric equipment demanded by most modern investigators. Not that such equipment has proved unproductive, but Parker's example will stand as an inspiration to those humble investigators who, forced to labor without handsome foundation grants, must depend upon their wit and ingenuity to devise experiments within the framework of their modest budgets.

Parker's demonstration of neurohumoral substances rests largely upon the behavior of so-called caudal bands in the tails of fishes. These are darkened strips running posteriorly from a small cut near the base of the tail. They are dark because the melanophores within them have expanded as a result of the severance of their connection with the central nervous system by the cut. After a time these darkened bands become pale and disappear. This paling Parker assumes to be due to the gradual diffusion into the denervated area of a concentrating neurohumor, presumably released from the chromoneural junctions in areas adjacent to the band. The concentrating neurohumor is presumed to be something very much like adrenalin.

No physiologist today would raise any strenuous objection to the theory that adrenalin can be released from the endings of certain sympathetic nerves and, under the proper occasions, in great enough amounts to affect the behavior of distantly removed effectors. Adrenalin, however, is generally considered to be a substance rather quickly destroyed in tissues, so quickly, in fact, that Parker's explanation cannot be true unless there is some means of preserving it. This Parker claims to be the case. In his opinion the released concentrating neurohumor is dissolved in the oily material of the tissues and in this state is protected against rapid destruction. Nowhere does Parker definitely say that the concentrating neurohumor is adrenalin, but it is clear that he thinks it is either adrenalin or something closely akin to it. Therefore one is asked to accept the possibility that a substance which is highly water soluble escapes destruction because it dissolves in the lipoids of the tissues.

On much less convincing evidence Parker assumes the dispersing neurohumor to be acetylcholine. As is well known, acteylcholine is even more rapidly destroyed in tissues than adrenalin. Parker again postulates that this water-soluble compound is protected against destructionn because it dissolves in the fatty material of the cells, thus

accounting for its prolonged action under certain conditions. If these statements be true, then adrenalin and acetylcholine may well act in other forms in ways previously unsuspected by other physiologists.

There is, however, an alternative possibility to explain the paling of caudal bands, which Parker does not seem to take into account. It is well known that end organs which are sensitive to adrenalin greatly increase their sensitivity after denervation and the subsequent degeneration of the myoneural junction. As has been shown, the fish melanophore is no exception. If such is the case, it is not necessary to postulate the solution of adrenalin in the oily constituents of the tissue to account for the paling of caudal bands. Their melanophores instead might well concentrate after sensitization by denervation to the amounts of adrenalin normally present in the circulating blood.

Parker assumes acetylcholine to be the dispersing neurohumor largely because of the demands of his theory of the double innervation of the fish melanophore. The main prop for such a claim is the observed dispersion of pigment in chromatophores after denervation. He claims this to be due to the discharge of impulses along the cut nerves, the dispersing nerves dominating over the concentrating nerves. His evidence for the existence of such a phenomenon is convincing but not direct. One wishes that an actual demonstration of action potentials in these cut nerves were possible, for the assumption that cut nerves are in a continuous state of activity up until the time they degenerate is one which most neurophysiologists would hesitate to make.

Even so, the melanosphores of fishes very probably receive a double innervation, but it does not necessarily follow, as Parker seems to think, that one set of nerves must be adrenergic and the other, cholinergic. Alternatively, both sets of nerves may be adrenergic. Such a situation would be comparable to what we see in some mammalian arterioles, where the vasodilator as well as the vasoconstrictor nerves are both adrenergic. Spaeth showed many years ago that the response of the melanophore in fishes to adrenalin could be reversed by ergot, just as can be the response of some arterioles in mammals. Adrenalin may either relax or contract smooth muscle since there is a high degree of probability that there are two kinds of adrenalin. It may very well do the same for melanophores. As a matter of fact, the nature of the dual nerve supply to fish melanophores requires a thorough study before any generalizations can be made as to its precise nature.

A great deal more might be said about this book, but enough has certainly been brought out to show how provocative it is. Such problems as whether the eye stalk hormone and intermedin are identical, why the eye stalk hormone concentrates the pigment of some crustacean chromatophores and disperses that of others, and whether there is a factor in the fish pituitary which concentrates pigment call for immediate investigation. This review has emphasized those problems associated with the color changes of fishes to the neglect of others, equally interesting and important, in connection with the behavior of chromatophores in the elasmobranchs, amphibians and reptiles, to say nothing of the crustaceans. It is not to be assumed from this that the problems in these fields are any less interesting or controversial. By all means let the reader find out for himself.—DIETRICH C. SMITH, University of Maryland Medical School, Baltimore.

THE STUDY OF PLANT COMMUNITIES. By Henry J. Oosting. W. H. Freeman and Company, San Francisco. 1948. 389 pp., 190 figs. $4.50.

The increasing realization of the importance of ecology to conservation, so admirably set forth in recent books by Vogt and other writers, has emphasized the need for an ecology text which would stress the ecological principles basic to an understanding of conservation. Oosting's book goes far toward satisfying this need. It is a well balanced text, written primarily from the phytosociological viewpoint, but with an adequate treatment of the individual factors of the environment.

The first part of the book is devoted largely to a description and discussion of the methods used in studying vegetation. The terminology follows that of Braun-Blanquet and the Montpellier school, but the various vegetational characters are illustrated with tables

and graphs from field studies of American communities. Throughout this and later sections there is a commendable restraint on the use of unnecessary and burdensome terms such as have cluttered the pages of most earlier plant ecology books.

The factors controlling plant communities are treated in four chapters—air, radiant energy, physiographic factors, and biological factors. While brief, the treatment is sufficient for beginning courses where time is an important element. The section on soils is especially thorough and in harmony with the most modern concepts. Unfortunately, the same cannot be said about the chapter on atmospheric factors, which touches only briefly on currently accepted principles of climatology.

The section of the book devoted to a description of the climax communities of North America discusses both their present distribution and their post-Pleistocene history. Excellent photographic illustrations accompany the accounts of each of the major plant associations of the United States. A suitable balance has been maintained in the treatment of Eastern forest, Central grassland and Western forest and scrub formations. Applied ecology in its various aspects is the subject of the last chapter. Forestry, land management, soil conservation, and wildlife management are effectively integrated with the ecological principles developed in earlier sections of the book.

The book is written in a clear and easily understandable manner, abundantly illustrated with well chosen photographs and drawings. It should find wide acceptance as a text for elementary courses in all parts of the country.—JOHN T. CURTIS, University of Wisconsin, Madison.

CHAMBERS'S MINERALOGICAL DICTIONARY with forty plates of coloured illustrations. Chemical Publishing Inc., Brooklyn, New York. 1948. 47 pp., new edition (first published 1945). $4.75.

It is difficult to understand the need for a mineralogical dictionary in view of the many excellent text and reference books both popular and technical in the expanded field of mineralogy.

This book consists of thirty-nine pages of definitions concerning mineral species and varieties, mineraloids, mineralogical physical and chemical properties, and petrology. The definitions are sufficient but the information will be inadequate to the student or practical mineralogist; whereas the novice will find it difficult to integrate the terminology. The forty colored plates which illustrate one-hundred sixty-three specimens representing one-hundred nineteen mineral species or varieties and five mineraloids, are indexed on pages six and seven. Obviously the relative high price for this small book has been the result of reproducing the color plates. These illustrations are fine but they would be of more value and greater benefit in a treatise on mineralogy. No attempt has been made to collate the plates with the text.

There is some merit to the publication in its alphabetic arrangement of mineralogical terms. It can be used as a short, handy reference.—R. C. GUTSCHICK, University of Notre Dame, Notre Dame, Indiana.

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The

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Founded by J. A. Nieuwland, C.S.C.

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